CONIFERALES (D.J. de Laubenfels, Syracuse, N.Y.)

General Introduction

In spite of generalized impressions sometimes advanced about the decline and decrease of the Gymnosperms through the enormous development of the Angiosperms in the Cretaceous and their rapidly accelerated development in the Tertiary, it must be realized that this impression is confusing as far as *Coniferales* are concerned.

It is of course a truism that the Gymnosperms are completely outnumbered in genera and species by the Angiosperms, the latter occupying terrain earlier beset by Gymnosperms. It must be realized, however, that possibly the almost entirely woody Gymnosperms did never have the potential for producing such immense numbers of genera and species as now found among the Angiosperms. This statement is also valid for the *Coniferales*.

The *Coniferales* were only part of the Cretaceous richness in Gymnosperms and whereas many Gymnosperm groups became extinct or lived on with meagre remains, *Coniferales* — though proportionally with few genera and few species — still represent a most essential part of the world's standing timber and involve a huge biomass through their sociability and their morphology: usually a large size and the little tapering of their cylindric boles.

The 'decline idea' is thus not valid for the *Coniferales* and this is further validated by their extremely wide ecological capacity, as they thrive from the Arctic to the Antarctic, in all major parts of the globe, in the lowland, the hills and the mountains, and in the tropics from the seashore almost to the alpine zone, a colossal range, among the Angiosperms shared or approached by only very few families, *e.g. Ericaceae* and *Fagaceae*.

This universal presence is also due to their most diverse ecological capacities. *Coniferales* are represented on the permafrost of the taiga as well as in hot semi-deserts, on all sorts of soils, from mineral-rich to mineral-poor, even in peat-swamps, enabling them to stand all sorts of environmental conditions.

In the forest vegetation they show not seldom a high power of competition, often leading to dominance or codominance, often coupled with longevity.

Some are agressive and tend to fill gaps in the vegetation by possessing nomad ecology.

Seed is mostly produced in ample quantity; seedlings may be shade-tolerant or -intolerant. A number of species are distinctly fire-resistant.

From these facts can be concluded that *Coniferales* are not just 'on the decline', but that they form still a most successful super-order of the Gymnosperms.

Distribution. With 12 genera the *Coniferales* are well represented in the Malesian tropics, while elsewhere in the world only in the rich Sino-Japanese flora is there a substantially larger concentration of conifer genera; nearby Taiwan for example has 15 genera (only four of which are shared with Malesia, *viz. Nageia, Podocarpus, Taxus,* and *Pinus*). Eight wide ranging conifer genera of Antarctic affinities are today well established throughout Malesia up to the westernmost margins and four of these extend well beyond onto the continental part of Asia (*Dacrycarpus, Dacrydium, Nageia*, and *Podocarpus*). All are strictly confined to rain-forest habitats.

Seven of these have seeds dispersed by birds, the eighth (*Agathis*) has small seeds with large membraneous wings. Except for the genus *Phyllocladus*, these genera are well represented at low and medium elevations and it is not necessary to imagine long-range dispersal between isolated mountain peaks as far as altitude is concerned. We have, however, to keep in mind that through the insular physiography of Malesia there may have been the necessity of crossing sea barriers. Unfortunately too little is known in detail about the precise distribution of land and sea in the course of the Tertiary.

Two Holarctic conifer genera (*Taxus*, *Pinus*) penetrate into western Malesia and two more Antarctic genera are at present confined to the eastern half of Malesia (*Libocedrus, Araucaria*). The fossil record, although incomplete, suggests that the situation was quite different as late as the Miocene.

Fossil record. Palaeozoic floras of Permo-carboniferous age are known from Sumatra and New Guinea. The Sumatra material shows affinities to Euramerican floras and, by the presence of *Gigantopteris* especially to the Cathaysian flora of Southeast Asia (JONGMANS & GOTHAN, 1935). In New Guinea fossil floras of Gondwana type as well as with a Cathaysian character are found (JONGMANS, 1940; LACEY, 1975), leading HAMILTON (1979) to suspect that at that time New Guinea was situated at mid-latitudes with land connections both to Sumatra and the Australian continent.

A Mesozoic flora dated as Neocomian (Lower Cretaceous) has been described by SMILEY (1970) from the Malay Peninsula. Although considerably poorer in species than the Palaeozoic ones, it is of interest because of the presence of two conifer genera, *Frenelopsis* of Cupressaceous affinity preserved as macrofossils and the fossil pollen genus *Classopollis*, derived from the extinct family of *Cheirolepidaceae*. *Frenelopsis* ranges from Lower to Upper Cretaceous and was widely distributed in North America, Europe and Asia. *Classopollis* is cosmopolitan and ranges from the Jurassic to the Upper Cretaceous. The general composition of this Lower Cretaceous flora clearly suggests links to Eurasian and North American floras.

MULLER (1968) has described a rich and well preserved Upper Cretaceous microflora from Sarawak, NW. Borneo, in which *Caytoniales (Caytonipollenites), Podocarpaceae (Zonalapollenites), Araucariaceae (Araucariacites), Cheirolepidaceae (Classopollis), Cupressaceae* or *Taxodiaceae (Inaperturopollenites)* and a rich assemblage of bisaccate pollen grains of Pinaceous or Podocarpaceous affinity represent the Coniferalean element. Although most of these genera are cosmopolitan, the presence of the bisaccate genus *Rugubivesiculites* is of considerable interest, since this has been recorded only from the northern hemisphere.

Tertiary floras from Malesia, which include both macro- and micro-floras, are mainly restricted to the post-Eocene and, for the Angiosperm component, show a composition not unlike the present one (KRÄUSEL, 1929; POSTHUMUS, 1929, 1931; ANDERSON & MULLER, 1975). However, the reliability of identification of many of these records, especially the older leaf remains, is questionable. An exception may be made for wood of *Dipterocarpaceae*, for which family also fossil pollen records are available, showing that, at least in the post-Eocene, this family was well established in West Malasia.

For Gymnosperms the situation is different and the presence of pollen of *Ephedra*, *Pinus*, *Picea* and *Tsuga* in the Oligocene and Miocene of NW. Borneo, accompanied by pollen of *Alnus*, its disappearance from the record at the end of the Miocene, followed by immigration of *Phyllocladus* and *Dacrycarpus* in the Plio-Pleistocene suggests considerable change in the coniferous elements in West Malesia (MULLER, 1966; STEIN, 1978). *Dacrydium* pollen, which was absent in the Upper Cretaceous-Paleocene assemblages studied by MULLER (1968) from Sarawak is first recorded for the Oligocene.

MULLER (*l.c.*) has attributed the disappearance of the Asian-montane element to peneplanation, but STEIN (*l.c.*) believes that they also may have suffered from competition with other forest elements in submontane habitats. Significantly, *Pinus* has survived longest in NW. Borneo and is still present today in N. Sumatra and the Philippines.

KHAN (1976) has established the presence of pollen of the following typical southern conifers in the Upper Miocene and Pliocene of New Guinea: *Dacrydium*, *Dacrycarpus* and *Microcachrys*, the latter disappearing from the record at the end of the Pliocene. Here the southern conifers are accompanied by *Nothofagus*.

This evidence indicates that, in Borneo, boreal conifers have been replaced by Antarctic ones, immigrating from the direction of New Guinea. *Dacrydium* may have reached western Malesia already in the Oligocene, while *Phyllocladus* and *Dacrycarpus* only reached Borneo in the Pliocene. In New Guinea the latter two were present earlier. This reflects the collision of the northwest moving Australian plate with the Celebes-Borneo area in the mid-Tertiary (HAMILTON, 1979; STEIN, 1978). Before this period Antarctic conifers may have been absent in West Malesia which has remained, at least since the Cretaceous, within reach of the Southeast Asian continent, as indicated by the presence of boreal conifers, both in the Cretaceous and Tertiary of the Malay Peninsula and Borneo. New Guinea presumably had been in close contact with Australia since the Palaeozoic.

From FLORIN's masterwork (1963) one could deduce that *Cryptomeria*-like conifers should have occurred in Malesia, since they are found fossil in the Triassic of both Asia and Australia, fading away in the early Cretaceous. Similarly, relatives of *Austrotaxus* of New Caledonia, *Athrotaxis* of Tasmania and various *Cupressaceae*, especially *Libocedrus*, all genera with Holarctic affinities, must have occurred in the Cretaceous of Malesia, inasmuch as these genera flourish beyond to the east and south. There are also reports of fossils belonging to *Podocarpaceae* and *Araucariaceae* from Holarctic regions and they could have migrated through Malesia at the same time, but only fossil *Araucaria* pollen is known from the Upper Cretaceous of Borneo.

The main conclusion from the fossil record is that, at least from the Lower Cretaceous onwards till the Oligocene, virtually no southern conifers reached West Malesia where in the Upper Cretaceous and, more strikingly, in the Oligocene and Miocene a distinct Asian conifer element was present. Only at the mid-Tertiary collision of Australia + New Guinea with West Malesia did an invasion of southern conifers take place, in stages leading to the present-day distribution pattern. However, it is clear that large gaps in our knowledge still exist and it seems most desirable to have reliable records from the Upper Cretaceous and Lower Tertiary of Java, Celebes, the Lesser Sunda Islands and New Guinea to allow a further confirmation of what is at present still a very tentative picture.

I appreciated very much the collaboration of the late Dr. J. MULLER (Leiden) in framing this paragraph on the fossil record.

References: ANDERSON & MULLER, Rev. Palaeobot. Palynol. 19 (1975) 291–351; FLORIN, Acta Horti Berg. 20(4) (1963) 121–312; HAMILTON, U.S. Geol. Surv. Prof. Pap. 1078 (1979) 1–345; JONGMANS, Meded. Geol. Bur. Mijngebied Heerlen 1938-1939 (1940) 263–274; JONGMANS & GOTHAN, Jaarb. Mijnwezen in Ned. Indië 1930, Verh. V.59, pt. 2 (1935) 71–201; KHAN, Austr. J. Bot. 24 (1976) 783–791; KRÄUSEL, Verh. Geol. Mijnbouwk. Gen. Ned. Kol., Geol. Serie II (1929) 1–44; LACEY in Campbell (ed.), Gondwana Geology, Austr. Nat. Univ. Press (1975) 125–134; MULLER, Blumea 14 (1966) 231–235; Micropaleontology 14 (1968) 1–37; POSTHUMUS, Bull. Jard. Bot. Btzg III, 10 (1929) 374–384; Leiden Geol. Meded. 5 (1931) 485–508; SMILEY, Geol. Soc. of Malaysia, Bull. *n.* 3 (1970) 77–113; STEIN, Biogeographica 11 (1978) 1–168.

Ecology. As mentioned above, the ecology of conifers shows a considerable variation and a summary may facilitate and stimulate the reader to delve in the text for further details.

No main vegetation type, except aquatics and very dry seasonal lowland, is in Malesia devoid of conifers. Though varying in density, they form an essential part of the forest and other vegetation. In the collecting numberlists of the Indonesian Forestry Service they form from one half to two percent of the total, depending on the area. Biomass of standing timber will attain probably a much higher percentage.

Conifers are among the tallest tree species in Malesia. Many possess massive straight boles, mostly cylindric, rising to or over the canopy with a height of 40–50 m. Some reach still larger dimension and tower as emergents over the canopy, equalling the tallest size of the largest *Dipterocarpaceae*; notably species of the genera *Agathis, Araucaria* and *Pinus* may reach 70–75 m in height, the occasional record being a tree of *Araucaria hunsteinii* of 89 m (B.GRAY, J. Ecol. 63, 1975, 273).

Small conifers are also well represented in Malesia. Mature specimens of no more than 1 m in height are found of *Nageia maximus* in Bornean swamp forests and of *Podocarpus micropedunculatus* on the edges of clearings in and near Brunei. Small conifers are also found in scrub in the mountains, *e.g. Dacrydium medium* on G. Tahan (Malaya). Colonies of prostrate *Podocarpus brassii var. humilis* occur on the mountains of New Guinea. Stunted specimens of many other species are found in poor, rocky habitats in the mountains.

Altitude. Lowland species are for example *Podocarpus polystachyus* which may be locally common (*e.g.* in Malaya) on sandy bluffs on the seashore and on low limestone outcrops. *Dacrydium pectinatum* and *D. micropedunculatum* can be locally common on low lying sand shoals (*e.g.* in S. Borneo), while the former along with *Agathis borneensis* may form nearly solid stands on lowland podsols (kerangas) or lowland peat-forest in Borneo almost at sea-level. The latter occurs sometimes in such quantity as to be worthy of exploitation for timber.

A genus 'descending' to low altitude is *Pinus*: in West Luzon and in Mindoro. *Pinus merkusii* reaches sometimes as low as 50 m altitude as a pioneer in pyrogenous grasslands and up to 150 m on volcanic ash streams (lahars) and lavastreams in N. Sumatra. Descent has also been reported for *Araucaria cunninghamii* on steep rocky ridges and spurs, occasionally as low down as 75–100 m, the 'normal' low parameter being *c.* 500 m.

With increasing elevation conifer populations become more frequent. At high altitudes species become fewer but it is not uncommon to find subalpine forest, whether or not turned into mossy forest, dominated by one or a few species of conifers. For example, the summit forest on Mt Leuser (N. Sumatra) is often dominated by a drooping conifer, *Dacrycarpus imbricatus var. curvulus*; on Mt Suckling (Papua New Guinea) *Araucaria cunninghamii* is the dominant conifer.

Climate. As mentioned above, in Malesia conifers shun the seasonally very dry *lowlands* of eastern Java and the Lesser Sunda Islands. They are also rather rare in the mountain rain-forest in this climatically seasonal belt, but *Dacrycarpus imbricatus* is found as far as Timor as a distinct constituent of the mountain forest; after devastation single trees may even survive as relicts in pyrogenous grassland, adorned with beards of *Usnea.*

Soils. Many conifers prefer nutrient-poor soils, and are often even confined to them, but there are also species which are mostly found on richer latosols, *e.g. Dacrycarpus imbricatus* which grows excellently on young volcanic soils.

As mentioned above, quite a number of conifers grow, sometimes in great quantity, on alluvial sandflats or on podsolized sands and sandstone (kerangas) and in peat-swamps, but they are not always limited to such habitat, as both *Dacrydium pectinatum* and *Agathis borneensis* are also commonly met as scattered individuals in middle elevation rain-forest.

Some conifers, particularly of the genus *Podocarpus*, thrive on ultrabasic bedrock in Malesia (as well as in New Caledonia), dense stunted forest with plenty of *Podocarpus confertus* in Borneo and *Podocarpus ridleyi* in Malaya are examples.

On Mt Soroako (Celebes) scattered specimens of *Agathis, Dacrydium, Podocarpus* and *Nageia* are found on ultrabasic bedrock. This may also be true for localized populations of *Podocarpus deflexus* of Malaya and N. Sumatra.

More precise data about possibly specialized soil types are unknown for a number of species with restricted ranges, *e.g. Podocarpus levis* in Central Malesia, *Dacrydium medium* in Malaya and Sumatra, *Dacrydium ericoides* in Borneo, *Dacrydium spathoides* in New Guinea, and *Agathis flavescens* in Malaya.

A curious conifer taxon is *Dacrydium cornwalliana* which is found in the mountains of West New Guinea (BW 697) restricted to deep black peat, reminding of the habitat of some *Dacrydium* and *Dacrycarpus* species occurring in peat under temperate conditions in New Zealand; both the former species and *Dacrycarpus steupii* are the only peat-swamp forest trees of Malesia sofar known. Fig. 14.

As to limestone, it can in general be said that conifers are rare on this bedrock. In western Malesia *Podocarpus polystachyus* occurs on low limestone outcrops; in Borneo and Celebes *Agathis* is also found on soils derived from limestone, and *Dacrycarpus imbricatus* is found on similar soils on Mt Perdido in Timor.

Autecology. In general Malesian conifers are constituents of the rain-forest and as such are dark-germinators, their seedlings growing up under very low light intensity. Germination and upgrowth of seedlings in shade is also the rule for high altitudes, but pioneering of conifers on disturbed, pyrogenous open land, at 2500–3000 m altitude was observed for *Libocedrus* and *Phyllocladus* by HOOGLAND.

A clear exception are the species of *Pinus, P. merkusii* and *P. kesiya*, which are light-demanding germinators. They may form permanent, dominant climax stands on very steep, rocky mountain slopes where no litter remains to prohibit germination. One can observe this on the Leuser massif in N. Sumatra at some 2500 m altitude. This occurrence is rare, the main occurrence is of a temporary nature, pioneers starting a succession, *viz.* bare soil of talus, volcanic mudstreams (lahars), lavastreams, earth- and rockslides, places torn open by earthquakes, and further man-made pyrogenous grassland. In the latter they occupy in W. Luzon and N. Sumatra large surfaces which are consequently converted into large, mostly savannah-like stands of *Pinus*. Under undisturbed conditions secondary forest and finally new primary forest will grow up among the pines, the litter and shade of which prohibits their own regeneration. But as *Pinus* is a long-lived pioneer, under such conditions the pines — which may possibly reach an age of 200–300 years — will remain towering over the later primary forest.

Seed of many tropical Malesian conifers rather soon loses its germination power, in line with other rain-forest trees. That of *Araucaria hunsteinii* is down to zero in ten weeks. According to WHITMORE the viability of seed of *Agathis* drops rapidly and also that of *Araucaria cunninghamii*. This is also valid for *Pinus merkusii*. On the other hand seed in *Podocarpaceae* may require as much as a year to germinate.

To the autecology also belongs the matter of the *mycorrhiza*, but unfortunately little is known of this relation. It is certain that one of the exomycorrhiza of *Pinus merkusii* is a *Boletus*, but it seems that for *Pinus* and probably other conifers more genera of fungi are involved. BEVEGE (1968) and HONG (Mal. Flor. 41, 1978, 225) have established that in the species of *Araucaria* an unidentified species of *Endogone* forms an endotrophic mycorrhiza.

Sociology. Mostly conifers occur scattered through the forest, but a number of species have a tendency to occur socially in places. By their large mature size they are then often observed as emergents. It must be remarked, however, that occurrences are often local: *Agathis* is for instance in Celebes above some 1600–2000 m (where it rather suddenly becomes abundant) and in the Moluccas present in most mountain forests and also in the north of West New Guinea, where it is tapped on a commercial scale, but in Papua New Guinea it is very scarce and local.

The same can be said of *Araucaria* in New Guinea, especially *A. hunsteinii*, which is found as an upper-canopy dominant in the Bulolo area and a few other places, but is elsewhere absent and not found in West New Guinea. In most instances we are ignorant about the underlying cause.

As mentioned above, *Podocarpus polystachyus* is locally common to subdominant in sandy lowland in Malaya and Borneo, and so are *Dacrydium pectinatum* and *Podocarpus micropedunculatus* in Borneo, where the former, sometimes together with *Agathis borneensis*, may form local stands on lowland podsols (kerangas) or in lowland peat-forest, with very acid soil conditions. *Agathis borneensis* may also form locally dense stands in the upper canopy. In passing we remark that hardly ever conifers are found in forest dominated by dipterocarps, with the possible exception of the heath-forest in Borneo. In the West Javanese mixed mountain forest (*e.g.* on Mt Gedeh) there are three large emergents very common: *Altingia excelsa (Hamam.)*, together with two conifers, *Dacrycarpus imbricatus* and *Podocarpus bracteatus*. But on Mt Tjeremai, a volcano in W. Central Java, there is between *c.* 1800–2500 m a very large gregarious dominant stand of *Dacrycarpus imbricatus* only. It remains unclear to what factor in the past this has to be ascribed.

In other islands other species of conifers may be very common or gain subdominance in the higher mountains. In Sumatra for example *Dacrydium elatum* – used for Christmas trees – and on Mt Leuser *Dacrycarpus imbricatus var. curvulus*, the drooping pine. A similar role in mountain forest is found with the dense stunted forests of *Podocarpus confertus* in Borneo and of *Podocarpus ridleyi* in Malaya on ultrabasic bedrock. Localized subdominance is found: *Podocarpus deflexus* and *Agathis flavescens* in Malaya, *Dacrydium medium* in Malaya and Sumatra, and *Dacrydium ericoides* in Borneo.

Mostly conifers occur scattered in the mixed broad-leaved rain-forest, not infrequently represented by several species; *e.g.* KALKMAN & VINK found on the Doma Peaks in Central New Guinea

Libocedrus papuana as an emergent, accompanied by *Dacrycarpus expansus*, *Phyllocladus hypophyllus*, and *Podocarpus pseudobracteatus* (Blumea 18, 1970, 119).

Anatomy. The most important wood anatomical surveys of *Coniferales* are by E.W.J.PHILLIPS, Identification of softwoods, For. Prod. Res. Bull. London 22 (1948, repr. 1966), and by P.GREGUSS, Identification of living Gymnosperms on the basis of xylotomy, Budapest (1955), Xylotomy of the living conifers, Budapest (1972). Additional data for Malesia and adjacent regions can be found in R.KANEHIRA, Identification of Philippine woods by anatomical characters, Taihoku (1924) 231–244; H.H.JANSSONIUS, Mikrographie des Holzes der auf Java vorkommenden Baumarten 6 (1936) 469–494; H.DESCH, Mal. For. Rec. 15 (1954) 630–632; M.KAEISER, Phytomorphology 4 (1954) 39–47; J.VAN DER BURGH, Rev. Palaeobot. Palyn. 15 (1973) 73–275; S.HAYASHI *c.s.*, Micrographic atlas of Southeast Asian timber, Kyoto (1973); T.FURUNO, Res. Rep. Foreign Wood 6, Shimane Univ., Matsue (1977); J.H.FUNDTER & J.H.WISSE, Meded. Landbouwhogeschool Wageningen 77-9 (1977); K.OGATA, Identification of Southeast Asian timbers (in Japanese), Jap. Ass. Wood Technology (1985).

Despite the seemingly homogeneous microscopic structure of the vesselless wood of conifers, there are a number of highly diagnostic wood anatomical differences at various levels of the taxonomic hierarchy which can be profitably used for identification and which can help in the reconstruction of a natural classification. In the Malesian representatives of the *Coniferales* a number of genera can be immediately recognized on unique, single or combined characters:

Pinus — Vertical and horizontal resin ducts present, cross field pits (*i.e.*, pits from tracheids to ray parenchyma cells) fenestriform or pinoid, ray tracheids present. (N.B.: resin ducts and ray tracheids are absent from all other Malesian *Coniferales*.)

Agathis and *Araucaria* — Pits on tracheids alternate and in a closely spaced honeycomb-like pattern ('araucaroid').

Taxus — Tracheids with distinct spiral thickenings.

Libocedrus — Cross field pits strictly cupressoid (*i.e.*, with narrow, included apertures).

Podocarpaceae — The distinction of *Podocarpaceae* from *Libocedrus* is fairly subtle: cross field pits in *Podocarpaceae* often include cupressoid types but almost invariably also other types such as taxodioid, pinoid, or piceoid pits. Most Malesian *Podocarpaceae* and *Libocedrus* have fairly common to abundant axial parenchyma in their wood, a feature absent from the other conifers. However, *Phyllocladus* and at least some temperate species of *Dacrydium* lack axial parenchyma. Presence or absence of parenchyma has been used as an important character for sectional delimitation in *Podocarpus sensu lato* by KAEISER, *l.c.*, but some of her observations have been contradicted in a more detailed study by R.N.PATEL, New Zeal. J. Bot. 5 (1967) 307–321. The evidence available from the literature at present suggests that the wood anatomical variation pattern within the *Podocarpaceae* does not coincide with generic delimitation; further studies of well-authenticated samples are needed to assess the taxonomic significance of the wood anatomical variation in this family.

Leaf anatomy can also play a useful role in identification and classification of the *Coniferales*, as exemplified in the study by J.T.BUCHHOLZ & N.E.GRAY, J. Arn. Arb. 29 (1948) 49–76 on the systematics of *Podocarpus sensu lato* and by J.W.LANYON, A card key to *Pinus* based on needle anatomy, Min. Conservation, N.S.W., Australia (1966), also including the two anatomically distinct Malesian species *Pinus merkusii* and *P. kesiya*. The extensive leaf anatomical literature on conifers is summarized in K.NAPP-ZINN, Encyclopedia of Plant Anatomy 8 (1), Berlin (1966). — P. BAAS.

Palynology. In general gymnospermous pollen is distinguished from angiospermous pollen by the alveolate-granular structure of the sexine, the lamellate structure of the nexine, and the presence of one distal aperture. With the exception of some primitive ranalean groups Angiosperms have pollen with a columellate sexine, a non-lamellate nexine, and 3 or more equatorial apertures, or have pollen with attributes that can be derived from this basic pattern. The structure of the sexine seems at present the most reliable character.

The only aperture in pollen of *Coniferales* is always distal. Mostly it is a thin area (leptoma) in the exine, which is often further distinguishable by a different ornamentation. In *Araucariaceae* this area is large and circular, in *Cupressaceae* and *Taxaceae* small and circular; in *Pinaceae* and *Podocarpaceae* it is mostly large and oblong. When large, the thin area may also have a harmomegathic function beside participating in the germination process. Sometimes an aperture is difficult to trace.

A remarkable feature of some *Coniferales* pollen types is the presence of air bladders (wings, sacci) at the distal pole beside the aperture. *Araucariaceae*, *Cupressaceae* and *Taxaceae* have none, but most *Pinaceae* (except *Larix, Pseudotsuga*) and *Podocarpaceae* (except *Saxegothaea*) have 2 or 3 of them. Grains without bladders are more or less spherical; those with bladders have a spherical, lens-shaped, or oblong corpus.

Most *Coniferales* pollen is medium-sized (25–50 μm). Pinaceous grains measure (40–)50–70 (–80) μm; the corpus of the likewise saccate podocarpaceous grains are mostly smaller (up to 50 μm). Both cupressaceous and taxaceous grains range from 18 to *c.* 36 μm. Araucariaceous grain size varies from 40–60 μm (*Agathis*) to 60–90 μm (*Araucaria*). In addition *Araucaria* pollen differs from that of *Agathis* by the presence of a proximal annular thickening.

There is a great deal of variation with regard to wall stratification and structure. *Araucariaceae*, *Cupressaceae*, and *Taxaceae* have a thick intine compared with the exine. In *Cupressaceae* the intine is even very thick, often comprising much more than half of the grain volume. A thick intine has the capacity of swelling after moistening and probably plays an important role in the germination process. In *Pinaceae* and *Podocarpaceae* the intine is proportionally less thick. The nexine is lamellate in all *Coniferales*. The sexine is alveolate-granular in *Araucariaceae*, *Cupressaceae*, and *Taxaceae*, in *Larix* and *Pseudotsuga* of the *Pinaceae*, and in *Saxegothaea* of the *Podocarpaceae*; in all the rest of the *Pinaceae* and the *Podocarpaceae* the sexine offers a columellate-tectate appearance superficially like the situation in Angiosperms, essentially being a variation of the alveolate structure. In *Pinaceae*, *Podocarpaceae*, and in most *Araucariaceae* pollen the sexine is thicker than the nexine, at least at the proximal side (cappa). In *Cupressaceae*, *Taxaceae*, and part of *Araucariaceae* pollen the nexine is the thickest layer. In the latter three families the surface of the sexine has a perine-like covering, consisting of small (< 1 μm) granules (orbicules), which is absent in *Pinaceae* and *Podocarpaceae*.

Air bladders or sacci form a remarkable aspect of the pollen wall of most *Pinaceae* and *Podocarpaceae*. Sacci develop by proliferation of the alveolate layer of the wall. Probably they function in both flight and harmomegathy of a grain. All *Pinaceae* have 2 sacci, except *Larix* and *Pseudotsuga* which are devoid of them and are fundamentally different from other *Pinaceae*. *Tsuga* mostly has pollen with one distal saccus encircling the aperture. In *Podocarpaceae* the genus *Saxegothaea* has no sacci and is therefore, and also on account of other features, considered as related to the *Araucariaceae*. In *Podocarpaceae* there is more variation in respect to the number, shape, and size of the sacci than in *Pinaceae*. Pollen grains of *Dacrycarpus* are provided with 3 sacci, those of *Nageia*, *Podocarpus*, and *Prumnopitys* with 2. *Phyllocladus* and *Falcatifolium* pollen also have 2 sacci, but in the first they are very small and in the latter they are narrowly connected around the aperture. In *Dacrydium* a type occurs which has one fully radiosymmetric saccus around the aperture. *Dacrydium* has also the *Podocarpus*-like bisaccate type. Saccate pollen of the *extra*-Malesian podocarpaceous genera has 2 sacci (*Acmopyle, Parasitaxus*) or 3 sacci (*Microcachrys, Pherosphaera*). In the latter two genera and in *Dacrycarpus* sometimes grains occur which have 4, 5 or 6 sacci due to aberrant tetrad configuration.

Pollen of the *extra*-Malesian *Cephalotaxaceae* and *Taxodiaceae* is largely similar to that of *Cupressaceae* and *Taxaceae*.

Coniferales are probably strictly wind-pollinated, the pollen being not sticky, smooth-surfaced, and sometimes provided with sacci. In the former two characters *Coniferales* pollen resembles some wind-pollinated Angiosperms (*e.g. Gramineae, Betulaceae*).

References: ERDTMAN, Pollen and spore morphology/plant taxonomy, Gymnospermae (1957)

5–44, illus., (1965) 9–82, text; POCKNALL, New Zeal. J. Bot. 19 (1981) 67–95, 259–266, 267–272; SIVAK, Pollen et Spores 17 (1975) 349–421; STAPLIN *c.s.*, Rev. Palaeobot. Palyn. 3 (1976) 297–310; TENGNÉR, Bot. Notis. 118 (1965) 450–452; VAN CAMPO, C. R. Acad. Sc. Paris 272 (1971) 2071–2074; WALKER, The evolutionary significance of the exine, Linn. Soc. Symp. Ser. 1 (1976) 251–308; WEND, J. Inst. Polyt. Osaka City Univ. 11 (1960) 109–136; WODEHOUSE, Pollen grains (1935). — R.W.J.M. VAN DER HAM.

Phytochemistry & Chemotaxonomy. Chemical characters of *Coniferales* were summarized twice in 'Chemotaxonomie der Pflanzen' (HEGNAUER, 1962, vol. 1: 293–440, 478–482; 1986, vol. 7: 462–554, 801–802). Here rather extensive bibliographies can be found for all families of *Gymnospermae, Cycadopsida, Coniferopsida, Taxopsida* and *Chlamydospermae.*

General characters of *Coniferales* are: cuticular waxes of the so-called estolide-type; lignin which usually lacks the syringyl component; seeds which store predominantly starch or oils with unusual fatty acids, *i.e.* bi-tetra-unsaturated C_{18}- and C_{20}-acids with an isolated double bond in 5-position; accumulation of cyclitols such as pinitol, sequoyitol and (or) 0-methylmucoinositol in leaves, bark and wood; storage of shikimic and (or) quinic acid in leaves; accumulation of lignans (phenylpropanoid dimers) and (or) agatharesinol-type norlignans in wood, bark, traumatic resins and leaves (here sometimes as glycosides); production and exudation after injury of oleo-resins or gum-resins.

Oleo-resins and gum-resins are deposited in schizogenic canals and cavities which seem to be lacking only in some representatives of *Taxaceae*. Oleo-resins are mixtures of essential oils and resins; turpentine is the essential oil produced by distillation of oleo-resins obtained from several species of *Pinus*. Gum-resins are mixtures of essential oil, resin and mucilage; *Araucaria* is the main producer of gum-resins among *Coniferales*. The predominant constituents of the essential oils of most *Coniferales* are mono- and sesquiterpenoids; some members of *Podocarpaceae* and other families produce appreciable amounts of steam-volatile diterpene hydrocarbons and hence yield diterpene-rich essential oils. The resins of *Coniferales* are mainly composed of diterpenoids; often diterpenic acids predominate. Colophony or rosin is the resin part of pine oleo-resins and Manila copal is the hard oleo-resin from *Agathis dammara*. Amber or succinite is the fossil resin of pines and Kauri copal is fossilized *Agathis* resin.

Tannins are ubiquitous in *Coniferales*. They are represented in the taxon exclusively by the so-called condensed tannins and their building stones, the catechins and proanthocyanidins. Galli- and ellagitannins are totally lacking.

Other classes of compounds which seem to be totally absent from *Coniferales* are iridoid compounds, cardenolides and steroidal saponins. The same seems to be true of triterpenoids of the ursane, oleanane and lupane classes, and hence of corresponding saponins.

Triterpenoids are represented in *Coniferales* by lanostane-type tetracyclic, onocerane-type tetra- and pentacyclic, and hopane-type pentacyclic compounds. Steroids are represented by the ubiquitous phytosterols; moreover, the frequent occurrence of phytoecdysones in rather high concentrations is somewhat typical of the taxon. In the products of steroid and triterpenoid metabolism *Coniferales* strongly resemble Pteridophytes.

Polyphenolic compounds other than lignans and tannins are accumulated by all conifers but, besides the general occurrence of flavonoids as a group, most classes of compounds and many individual compounds are restricted to taxa of lower levels such as infrageneric, generic and suprageneric entities. The same is true of alkaloids and several other classes of chemical constituents. Some examples to illustrate the situation follow.

Agathisflavone-, amentoflavone-, cupressuflavone-, robustaflavone- and hinokiflavone-type biflavones seem to be nearly ubiquitous in leaves of Gymnosperms, but are lacking in *Pinaceae* which yielded hitherto only one biflavonoid, the flavone-flavonol dimer abiesin.

Cephalotaxin-type alkaloids occur in all species of *Cephalotaxus*.

All members of the genus *Taxus* (but not the other representatives of *Taxaceae*) produce taxane-type diterpenoids which are often esterified with the so-called Wintersteiner acid, which is a dimethylamino derivative of a hydroxydihydrocinnamic acid; the resulting nitrogen-containing constituents, such as the taxines and related compounds, are the 'Taxus alkaloids'; they are accompanied in *Taxus* by the cyanogenic glucoside taxiphyllin. The latter too seems not to occur in other genera of *Taxaceae*, but is present in *Metasequoia* and in some species of *Juniperus*.

In *Podocarpaceae* several tendencies concerning secondary metabolism are recognizable: essential oils with appreciable amounts of diterpene hydrocarbons, ferruginol- and totarol-type phenolic diterpenes, bitter and biologically highly active mono- and bisnorditerpenoid lactones such as nagilactone, and accumulation of large amounts of phytoecdysones such as the makistrones and the podecdysones are examples of such family-characteristic tendencies. At the same time the family is the only representative of conifers which makes use of anthocyanins to advert its diaspores: red to pink fleshy parts of *Dacrydium*, *Phyllocladus*, and *Podocarpus* diaspores contain an array of anthocyanins; anthocyanins may also be present in young leaves and strobili; the latter feature is not restricted to *Podocarpaceae*, however.

Antibiotically active carvacrol and thymol derivatives and tropolone-type mono- and sesquiterpenic compounds are present in the wood of many *Cupressaceae*, including *Libocedrus s.l.*

Exudates of many species of *Araucaria* contain larger amounts of mucilage than most other conifers; they are true gum-resins; ANDERSON and MUNRO observed 20–80% of mucilage in *Araucaria*-exudates with 10–20% of uronic acids, 50–70% galactose and up to 7% of the rather unusual sugar acofriose (3-0-methylrhamnose) as building stones. Acofriose is also present in mucilages of *Cycadaceae*.

An array of low-molecular phenolic compounds, such as hydroxyacetophenones, stilbenes, dihydrostilbenes and phenylpropanoids (monolignols) is known from *Pinaceae*; they occur free and as glycosides and often have a taxon-characteristic distribution, and hence can be useful as taxonomic characters. Pinosylvin and its monomethyl ether have been interpreted as phytoalexins of *Pinus* because their synthesis is induced in the softwood after infection; normally these antifungal compounds are present in *Pinus* only in hardwoods and in barks.

Flavonoid patterns were taxonomically exploited by many phytochemists; flavonoids yielded characters applicable at all levels of the taxonomic hierarchy. Just one example: C-glycoflavones have not yet been traced in *Araucariaceae, Cephalotaxaceae, Cupressaceae* and *Taxaceae*, and seem to be restricted in *Pinaceae* to *Abies, Keteleeria, Tsuga* and *Larix*; moreover, they were detected in *Podocarpaceae* in some species of *Podocarpus*.

In recent times detailed analyses of essential oils were performed during biosystematic studies of a number of American conifers; the results proved to be rather promising; in many instances a better understanding of complex population structures was made possible by such investigations.

As a whole *Coniferales* are chemically well characterized by the general presence of several classes of chemical constituents and by the total absence of others. Moreover, secondary metabolites yielded a large number of characters applicable at different levels of the taxonomic hierarchy. — R. HEGNAUER.

Systematics. *Generic delimitation.* Four genera replace earlier broad treatments of the genus *Podocarpus*, all of which I recognized in 1969 (J. Arn. Arb. 50: 274–369); in part they had formerly been distinguished as sections of this genus. Certainly there exist substantial relationships between them, but it must be well recognized that this is no sufficient reason for adopting a one-genus concept for the whole. As a matter of fact the morphological differences between these sharply distinct genera are at least of equal taxonomic 'weight' as compared to the differences between many other groups of northern hemisphere coniferous genera unequivocally distinguished. On the other hand I cannot adhere to the recent splitting of the genus *Libocedrus*. For further argumentation I refer to the text under the genera in the taxonomic part.

Cultivation. A fairly large number of exotic conifers are cultivated in Malesia, in part for testing them for forestry purposes, reafforestation, in part as ornamentals in gardens and parks.

It falls outside the scope of this Flora to treat the cultivated exotics like the native species, none of them is naturalized. Quite some have been incorporated in BACKER & BAKHUIZEN VAN DEN BRINK's Flora of Java (Vol. 1, 1963, 87–95) which may be useful for their identification. A more general work that I can advise for identifying cultivated conifers is W. DALLIMORE & A.B. JACKSON, A handbook for Coniferae and Ginkgoaceae, 4th ed., revised by S.G. HARRISON (1966).

Of native conifers several are in cultivation for various purposes. *Agathis philippinensis* is frequently cultivated as a wayside tree in W. Java and probably elsewhere, and occasionally found in parks. *Araucaria cunninghamii* is frequently planted in parks and gardens as an ornamental tree. *Araucaria hunsteinii*, of which very large dominating complexes are found in some places in the Bulolo area in Papua New Guinea, is exploited from native growths, but the cleared territory is replanted with it on a large scale, because of the valued timber used for plywood. *Dacrydium elatum* is, according to CORNER, widely planted in the hills in Malaya for ornamental purpose. Finally *Pinus merkusii* is widely used for reafforestation and in addition for timber and the tapping of resin for the turpentine industry; notable huge complexes are found at Aek na Uli on the eastern hills around Lake Toba in N. Sumatra; large complexes are also found in S. Celebes; it is also used as an ornamental in parks and gardens.

In nurseries, especially of *Agathis*, a single specimen of an older seedling already provided with mycorrhiza is planted in the centre of the beds in order to speed upgrowth of seedlings.

An important point for silviculturists is the fact that, as mentioned above, the seed of many tropical conifers soon loses germination power. For *Pinus merkusii*, which is distributed on a large scale, very special care must be taken to keep the sundried seed in sealed metal containers with charcoal; even with these precautions a rather rapid loss of germination power takes place. This has been subject to extensive study. Keeping seed storage cooled is also applied.

The timber of the large-sized species of all genera is most valuable, but only few are planted for this purpose on a large scale. This is in part due to the fact that of most species growth is slow, with the exception of *Pinus* species. It depends also for what purpose the timber is used, for pulp, sawn timber or high quality veneer. WHITMORE mentioned for *Agathis* in Java a rotation period of 30 years for pulp, and 50 years for veneer. For *Araucaria* in New Guinea a rotation period of 60 years is reckoned for plywood.

Economic uses. As mentioned above all larger species of all genera provide excellent timber. In addition, species of *Agathis* are tapped large-scale, especially in the Moluccas and New Guinea, and to a less extent in Borneo and Celebes, for the resin ('copal' or 'manila copal', wrongly 'damar'). In addition to the resin obtained from living trees, large bodies of subterranean resin of vanished trees are collected. The market for manila copal declined after the introduction of oil-based synthetics but there is still a use for special purposes.

The resin of *Pinus merkusii*, and to a less extent that of *P. kesiya*, is collected for the turpentine industry. In N. Sumatra, in the vicinity of Takengon, there was a large factory for this purpose. See C. BRANDTS BUYS *c.s.* (Meded. Proefstation Boschwezen 19, 1928).

References in synonymy. A remark must be made about the references in the synonymy of the species. I have omitted in many cases the mention of names without description or notes which occur in so many local plant lists and casual enumerations. This was made especially urgent by the fact that the names used in these lists, *e.g.* of *Agathis* and *Podocarpus*, are often wrong according to my classification. To account for all these *'non'* or *'sensu'* names would have caused an unnecessarily complicated synonymy. If collectors' numbers were cited in these local lists, proper identity of these records can easily be checked by means of the 'Identification Lists of Malesian Specimens' *n.* 61 (1982), which was issued separately by the Rijksherbarium, Leiden.

KEY TO THE FAMILIES
based on sexual characters

1. Ovules strictly terminal on short fertile shoots, erect, wingless. Pollen sacs usually several on each microsporophyll. Two single trace cotyledons .... **Taxaceae**
1. Ovules produced on axillary structures of a fertile shoot.

2. Seed usually cupped by a fringing epimatium or the inverted seed even completely enclosed by a leathery or fleshy structure, rarely naked and rarely erect, solitary, wingless. Reduced cone bracts often fleshy. Two pollen sacs on each microsporophyll. Cotyledons usually two fused pairs, occasionally more **Podocarpaceae**
2. Seed produced on an erect, woody, rarely fleshy scale which is often fused with the fertile bract, erect or inverted, occasionally solitary, more often two or more per fertile scale, usually with one or more wing(s).
3. Fertile bract and scale fused, sometimes indistinguishable. Seeds solitary or in variable numbers. More than two pollen sacs on each microsporophyll. Cotyledons usually 2–4.
4. Seed inverted, solitary; large mature seed cones disarticulate. Leaves spirally placed or opposite-decussate and distant. Cotyledons four or two fused pairs .... **Araucariaceae**
4. Seed erect, solitary or in variable numbers; small mature seed cone does not disarticulate. Leaves crowded, opposite-decussate or whorled. Cotyledons two or occasionally more, not fused. . **Cupressaceae**
3. Fertile bract separate from scale and not woody. Seeds two per scale, inverted, each with a single wing. Two pollen sacs per microsporophyll. Leaves spirally placed. Cotyledons more than two . . **Pinaceae**

ARTIFICIAL KEY TO THE FAMILIES
based on vegetative characters

1. Leaves spirally attached, sometimes distichous.
2. Leaves (needles) in bundles of 2–3 with a basal sheath (*Pinus*) .... **Pinaceae**
2. Leaves not in bundles with a basal sheath.
3. Leaves needle-like or scale-like.
4. Leaves scale-like (*Dacrycarpus, Dacrydium*) .... **Podocarpaceae**
4. Leaves needle-like, triangular or quadrangular in cross-section.
5. Tree with a very dominant primary trunk with regularly placed whorls of lateral branches. Seeds dry, in large bracteate cones (*Araucaria cunninghamii*) .... **Araucariaceae**
5. Tree quite irregularly branched. Seeds few, in reduced cones (*Dacrycarpus, Dacrydium, Falcatifolium*) **Podocarpaceae**
3. Leaves distinctly flattened and often broad.
6. Leaves bifacially flattened, linear, less than 2.5 mm wide, with a basal constriction (*Taxus*) **Taxaceae**
6. Leaves if linear either bilaterally flattened, or more than 2.5 mm wide, or without a basal constriction (*Dacrycarpus, Falcatifolium, Phyllocladus, Podocarpus, Prumnopitys*) .... **Podocarpaceae**
1. Leaves decussate, often distichous.
7. Leaves scale-like (*Libocedrus*)... **Cupressaceae**
7. Leaves broad and many-veined.
8. Leaves sessile, clasping, lanceate from a broad base (*Araucaria hunsteinii*) .... **Araucariaceae**
8. Leaves broad, not with a stem-clasping base.
9. Terminal bud hemispherical (*Agathis*) .... **Araucariaceae**
9. Terminal bud acute (*Nageia*) .... **Podocarpaceae**

TAXACEAE

The affinity of *Taxaceae* has been much debated, with many authors favouring a separate order, *Taxales*, for it, a position with which I tend to agree. Further questions are raised concerning the grouping of other families with *Taxaceae*, as against the other conifer families, based on the lack of seed cones, fleshiness of the mature fruit, or lack of a fertile seed scale. *Cephalotaxaceae* (not in Malesia) has a reduced seed cone structurally organized quite differently from other conifers and vegetatively strongly resembling *Taxaceae*, so I would group these two together. All other conifer families show seed structures easily derivable from a compound cone with ovules produced on the upper face of a fertile scale which grows in the axil of a bract. Although *Taxaceae*, perhaps joined by

Cephalotaxaceae, can be set apart from the conifers proper, all can agree that taxads and conifers are more closely related to one another than to any other recognized group.

Distribution. Of the five genera recognized for the *Taxaceae*, only *Taxus* reaches Malesia. Four are distinctly Holarctic in distribution, including *Taxus*, which is much the most widespread and reaches into tropical highlands. The fifth, monotypic *Austrotaxus*, appears on the other side of Malesia in New Caledonia, a distinct fragment of Gondwanaland, obviously a most curious relict on the southern hemisphere (FLORIN, Acta Horti Berg. 20 (4), 1963, 260, f. 61: map).

1. TAXUS

LINNÉ, Gen. Pl. ed. 5 (1754) 462; Sp. Pl. 2 (1753) 1040; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 110; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 208; FLORIN, Acta Horti Berg. 14 (1948) 378; GAUSSEN, Gymn. Act. & Foss. fasc. 15, ch. 25 (1979) 2. — **Fig. 2, 3.**

Evergreen trees or (prostrate) shrubs. Bark thin, smooth, purple-red, peeling in large thin flakes. *Leaves* spirally placed (but usually twisted into a single plane), linear to linear-lanceolate, acute, distinctly constricted at the base where the leaf twists into a horizontal position and then widening again in the decurrent part, penetrated by a single vascular strand marked on the lower surface by a blunt ridge which separates two bands of stomata and on the upper stomata-free surface by a sharp narrow ridge. Foliage and fertile buds small and globular, formed by several small keeled overlapping scales, the lower ones of which remain small while the higher ones expand with growth to become round and membranous. Usually dioecious. The *fertile structures* produced in the axils of ordinary leaves. *Pollen cone* solitary above a basal cluster of sterile scales, each peltate microsporophyll with a symmetrical whorl of 6–8 inverted pollen sacs, one microsporophyll in a terminal position and up to a dozen spirally placed lateral microsporophylls. *Seed-bearing structure* compound with one or more short ovule-bearing shoots produced subterminally on a very short fertile axis covered by minute keeled spirally arranged scales, each fertile shoot consisting of several decussate pairs of keeled scales which expand as the seed matures into a broad membranous oval shape and together cover the base of the ripened fruit. A small *basal aril* gradually grows to cup the single erect terminal seed, finally becoming fleshy and bright red. *Mature seed* flask-shaped, slightly wider than thick with the wider margin slightly keeled.

Distr. Seven species on the northern hemisphere middle latitudes and some tropical highlands, almost completely allopatric, but possibly some overlap between two species in the eastern Himalayas; one species in *Malesia*, and that one more common in subtropical parts of China. The genus has a predominantly northern hemisphere distribution, Central America and S. Celebes being the stations at lowest latitude. Fig. 1.

Fossil remains are known from Europe (middle Jurassic to Pliocene) and eastern Asia (Miocene to Pliocene).

Ecol. Understory or canopy plants of moist temperate or tropical mountain forest. From near sea-level in their northernmost occurrence in Norway they reach to nearly 3000 m in subtropical and tropical mountains

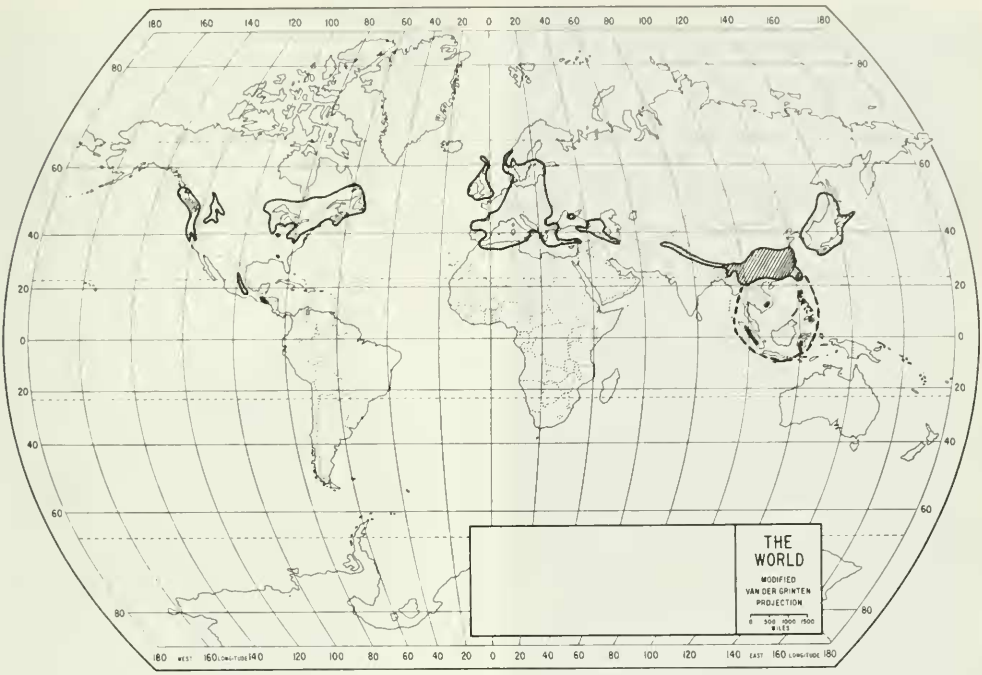

Fig. 1. Range of the genus *Taxus L.* (solid line) and *T. sumatrana* (MIQ.) DE LAUB. (broken line and hatched).

and do not go below 1200 m in tropical latitudes. As an undershrub they can be locally quite common, but the trees in this genus rarely take a dominant canopy role. Growth is generally quite slow but dense and specimens are often prized as ornamentals. Even the forms which are capable of becoming immense trees usually appear as shrubs or at best as small trees when under cultivation.

Pollination is strictly by wind dispersal. Fruits are taken by birds and probably other animals. The seeds are bitter and poisonous when broken into, so that the seeds are normally ingested intact and efficiently dispersed in animal droppings. Seeds germinate readily in moist shady places.

Seedling foliage is essentially similar to that of the adult. Vigorous young plants tend to have leaves larger than those of fully mature specimens, up to two and three times as large and sometimes more lanceolate and falcate.

Taxon. All seven species are closely related and some, at least, hybridize readily. As a result some authors such as PILGER prefer to recognize but one species with several subspecies. I would need to know more about the relationships between the taxa before I could take a strong position in this case.

Uses. The tough, dense wood has excellent qualities and has been in demand for many uses. Best known is its service for bows and decorative woodwork such as chests and coffins. It is also desirable for fence posts, flooring, and mallots. The well-marked reddish brown heartwood contrasts pleasingly with the pale yellowish sapwood.

1. **Taxus sumatrana** (MIQ.) DE LAUB. Kalikasan 7 (1978) 151. — *Cephalotaxus sumatrana* MIQ. Fl. Ind. Bat. 2 (1859) 1076. — *Podocarpus celebicus* HEMSL. Kew Bull. (1896) 39. — *Cephalotaxus celebica* WARB. Monsunia 1 (1900) 194. — *Cephalotaxus mannii* (*non* HOOK.*f.*) PRITZEL *ex* DIELS, Bot. Jahrb. 29 (1900) 214; WILSON, J. Arn. Arb. 7 (1926) 40. — *T. baccata* (*non* L.) MASTERS, J. Linn. Soc. Bot. 26 (1902) 546, p.p. — *T. baccata ssp. cuspidata var. chinensis* PILGER, Pfl. R. IV, 5, Heft 18 (1903) 112; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 210. — *T. baccata ssp. wallichiana* (*non* ZUCC.) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 112; BÜNNEMEIJER, Trop. Natuur 10 (1921) 55, f. 8; STEEN. Bull. Jard. Bot. Btzg III, 13 (1934) 194; STEUP, Trop. Natuur Jub. no. (1936) 41, f. 1. — *T. baccata var. sinensis* HENRY in Elwes & Henry, Trees Gr. Brit. & Irel. 1 (1906) 100. — *T. wallichiana* (*non* ZUCC.) FOXW. Philip. J. Sc.

Fig. 2. *Taxus sumatrana* (MIQ.) DE LAUB. on the peak of Mt Bonthain, Celebes, 1700 m alt. (Photogr. J.VAN ZIJLL DE JONG, 1933).

6 (1911) Bot. 166; MERR. En. Philip. Fl. Pl. 1 (1923) 5; YAMAMOTO, J. Soc. Trop. Agric. 10 (1938) 182, f. 42. — *Tsuga mairei* LEMÉE & LÉVEILLÉ, Le Monde des Plantes, année 16 (2me sér.) *n.* 88 (May 1914) 20; Bull. Acad. Int. Geog. Bot. 16 (1914) 20. — *T. cuspidata var. chinensis* (PILGER) REHDER & WILSON in Sargent, Pl. Wils. 2 (1914) 8, *p.p.* — *T. cuspidata* (*non* SIEB. & SUCC.) KANEH. Formos. Trees (1917) 616. — *T. chinensis* (PILGER) REHDER, J. Arn. Arb. 1 (1919) 51; *ibid.* 4 (1923) 119; DALLIMORE & JACKSON, Handb. Conif. (1923) 71; WILSON, J. Arn. Arb. 7 (1926) 41; *ibid.* 8 (1927) 88; HAND.-MAZZ. Symb. Sin. 7 (1929) 2; HU & CHUN, Icon. Pl. Sin. 2, 8 (1929) pl. 53; BEAN, Trees & Shrubs Brit. Is. 3 (1933) 476; ORR, Not. R. Bot. Gard. Edinb. 18 (1933) 124; *ibid.* 19 (1937) 261; KANEH. Formos. Trees rev. ed. (1936) 31; REHDER, Man. Cult. Trees & Shrubs 2 (1940) 3; METCALF, Fl. Fukien 1 (1942) 23; FANG, Icon. Pl. Omeiens. 11, 2 (1946) t. 190; LAW, Bot. Bull. Acad. Sin. 1, 2 (1947) 143. — *T. wallichiana var. chinensis* (PILGER) FLORIN, Acta Horti Berg. 14 (1948) 378, pl. 5; GAUSSEN, Gymn. Act. & Foss. fasc. 15, ch. 25 (1979) 16. — *T. speciosa* FLORIN, Acta Horti Berg. 14 (1948) 382, pl. 6; LI & KENG, Taiwania 1 (1954) 29, pl. 2. — *T. mairei* (LEMÉE & LÉVEILLÉ) HU & LIU, Illus. Nat. & Introd. Lign. Pl. Taiwan 1 (1960) 16; GAUSSEN, Gymn. Act. & Foss. fasc. 15, ch. 25 (1979) 16, f. 858. — *T. celebica* (WALL.) LI, Woody Fl. Taiwan (1963) 34; HARRISON, Handb. Conif. & Ginkgo (1967) 598. — *T. yunnanensis* CHENG, CHENG & FU, Acta Phytotax. Sin. 13 (4) (1975) 86. — **Fig. 2, 3.**

Fig. 3. *Taxus sumatrana* (MIQ.) DE LAUB. Habit, female, with fruit, × 1 (DE LAUBENFELS P668).

Large, slow-growing tree to as much as 45 m high and over 1 m diam., but considerably shorter on exposed ridges. *Leaves* on juvenile specimens or on vigorous shoots linear lanceolate and often falcate with a prominent bend near the base and also sometimes with a slight reverse curve near the apex which is narrowly acute and often slightly spiculate, 2–4 cm long by 2–2.5 mm wide at the widest part below the centre of the leaf. Leaves on older specimens or from exposed positions more nearly linear and straight and abruptly narrowed at the apex, 1.5–2.5 cm by 1.5–2 mm, with slightly recurved margins. *Pollen cones* globular on a short stalk, about 4 mm in diameter. Mature *seed c.* 6 by 5 mm, and 4 mm thick.

Distr. Eastern Himalayas, N. Burma, SE. China, Taiwan, South Vietnam; in *Malesia*: Sumatra (from Karoland southwards to Benkulen), Philippines (Luzon: Lepanto, Benguet, Laguna, Tayabas; Mindanao; Davao), Celebes (Central and SW.: Bonthain Peak). Fig. 1, 4.

Ecol. Moist subtropical forests and tropical highland ridges and mossy forests in the canopy and locally dominant; 1400–2300 m.

Uses. A magnificent timber tree, but occurring too locally to be of importance and too slow-growing for cultivation.

Vern. *Tampinur batu*, Karo, *kaju tadji*, Mt Dempo.

Note. The extensive synonymy partly stems from the discontinuous distribution, but several authors insist that two types exist in China. Whereas immense trees are seen in undisturbed forests of Taiwan and in Malesia, on the mainland only smaller trees are normally seen with one type reported mostly at lower elevation and another at higher elevation. Both types, however, often appear from the same collection area and I was able to collect both from a single large Formosan tree, part from low on the tree and part from high up. It appears that trees rarely get beyond their early stages of growth in lowland China, while highland trees, as is usual elsewhere, are of much reduced stature.

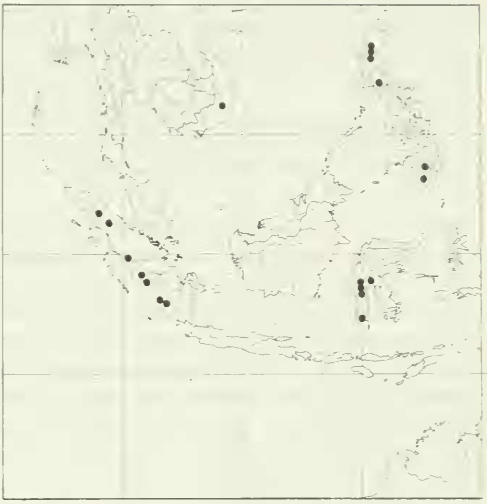

Fig. 4. Range of *Taxus sumatrana* (MIQ.) DE LAUB.

PODOCARPACEAE

Monoecious or dioecious trees and shrubs, some prostrate (and one parasitic on another member of the family, *Parasitaxus*, in New Caledonia). Each cotyledon, of which there are usually two but in a few cases more, a fused pair with a corresponding bifid tip. Foliage buds ranging from a loose cluster of reduced leaves to a complex specialized structure (in *Podocarpus*). *Leaves* of many shapes and sizes. *Pollen* produced in small cones with many microsporophylls, each of which have two inverted dorsal pollen sacs above which is a small sterile tip. *Male cones* may be solitary in the axils of ordinary leaves, sometimes many adjacent cone subtending leaves, or they may be terminal or clustered on special structures involving sterile scales, or in a few cases they may arise in the axils of scales at the base of a new foliage shoot. The *pollen* for all genera (except *extra*-Mal. *Saxegothaea*) is provided with two or more bladders or 'wings', a trait shared with many genera of *Pinaceae*. More than two are found only in *Dacrycarpus* (and *extra*-Mal. *Microcarpus* and *Microcachrys*). The basic *seed producing structure* in *Podocarpaceae* is a compound terminal or lateral cone in which fertile scales arise in the axils of cone bracts. The cone is further often subtended by a specialized shoot with scales or modified leaves or even a naked peduncle. The bract is usually a small scale but may be larger and in some cases hardly differs from foliage leaves. The fertile scale or epimatium is a highly modified shoot and in this family bears a single naked ovule on its upper surface. In one genus there is no scale while this and one other genus have erect ovules, but in the great majority of genera the ovule is inverted. The *fertile scale* cups the developing seed and may even completely surround it with only the micropyle protruding at the time of pollination. Fleshiness, either of the cone bracts or of the fertile scale (or both) is common and the whole female structure may be reduced to only one or a few fertile units and a few sterile units. This can yield plum-like fruits or, in other cases, structures resembling those of the cashew (*Anacardium occidentale*).

Distribution. There is a strong Antarctic relationship with a broad extension into Malesia for the 172 known species in 13 genera (in *Malesia* 7 genera with 61 *spp.*). Of six local and generally primitive genera, four are in the Antarctic zone and two are in New Caledonia. Three wide-ranging genera extend also into the tropical American highlands and two of these further range across the tropical African highlands. All seven of the wide-ranging genera are common in Malesia, only one of which (*Falcatifolium*), however, is confined to the Asian tropics; five are in New Zealand. A few species reach into moist subtropical forests of eastern Asia.

Fossils. The early fossil record is quite limited unless one includes forms that merely resemble the *Podocarpaceae* and whose relationships range from uncertain to highly doubtful. Suggestive macrofossils and pollen of the Jurassic indicate that the family was probably already present in India as well as in the far southern latitudes including New Zealand and W. Antarctica, that is to say Gondwanaland. Similar finds continue through the Cretaceous except for India, where Podocarpaceous fossils no longer occur. In the Eocene and Oligocene, fossils of this family become more abundant in the higher southern latitudes and can often be assigned to modern genera. Fossils, particularly pollen, show that some of the presently endemic genera such as (*extra*-Mal.) *Acmopyle* and *Microcachrys* were formerly of much greater distribution.

Some recent authors insist that fossils of *Podocarpaceae* occur in boreal regions. FERGUSON (1967) identified *Podocarpus* among Cenozoic fossils from Europe, suggesting a recent wider preglacial expansion of the genus. REYMANOWNA (1975) recently recognized *Dacrydium* and *Stachycarpus* (*Prumnopitys*) from the Jurassic of Europe. Furthermore, I have been told by palynologists that typical *Podocarpaceae* type pollen is well represented in northern latitudes. On the other hand, FLORIN (1963), after having examined both such alleged macrofossils and pollen fossils, expressed strong scepticism concerning their relationship to *Podocarpaceae* while pointing out that southern hemisphere strata are rich in Podocarpaceous remains. Certainly if any such plants ever existed beyond subtropical China and India, they have since disappeared completely while primitive forms of the family now survive only in the far south where they also have a respectable fossil history.

Fossil and present-day distributions suggest that the *Podocarpaceae*, as we know it, developed in cool moist Antarctic forests early in the Mesozoic period. Modern genera were already differentiated before the parts of Gondwanaland became isolated. Several genera had reached India and Kerguelen where they eventually disappeared, but two genera still survive in Africa. All of the important genera were included in the South American landmass where one interesting endemic genus, *Saxegothaea*, is also still found, but some of the other genera have since become extinct there. Probably all the recognized living genera had already differentiated before the Tertiary as a major element of the Antarctic flora. Only in Malesia and probably only in late Tertiary times have members of this family descended into the lowlands of the tropics to any significant extent. They are still a major element not only in the Antarctic forests and in the Malesian highlands, but also in the tropical highlands of Africa and America.

Maps of fossil distribution are given by COUPER (1960) and FLORIN (1963).

References: COUPER, Proc. R. Soc. Lond. ser. B, 152 (1960) 491–500, maps; FERGUSON, Palaeogeogr., Palaeoclimatol., Palaeoecol. 3 (1967) 73–110; FLORIN, Acta Horti Berg. 20 (4) (1963) 121-312, 68 maps; REYMANOWNA, XIIth Intern. Bot. Congr., Leningrad; Abstracts (1975) 99.

Ecology. Mostly trees of moist forests at all elevations and well into the middle latitudes both as major canopy trees and as understory plants, rarely in areas with a marked dry season. A few species are scrubby or even prostrate and as such may be found beyond the tree line, on rocky outcrops or other specialized habitats. The family is well represented in, but not confined to difficult soils such as sand and ultrabasics as well as in mossy forests.

There are nodules regularly present on the roots, but their function is unclear. FURMAN (Amer. J. Bot. 57, 1979, 910) showed that they contained endotrophic mycorrhizae and that nitrogen fixation did not occur. BECKING (Ann. Inst. Pasteur. 111, 1966, 295) indicated that the mycorrhizae were *Phycomycetes*. Growth is possible in sterile soil without mycorrhizae.

Most genera are dioecious and pollination is by wind. Individuals are usually scattered but locally common and the large quantities of pollen that are often produced seem to be able to reach effectively across considerable distances. Seedlings are found scattered and even quite isolated from seed sources due no doubt to dispersal by birds or fruit bats which eat the fleshy fruit. Coordination of fruiting times is for many species in tropical regions not well developed because at any given time it is often possible to find examples at any and all stages of reproduction and the collection of ripe fruit is variously reported for a given species at disparate dates. I have even seen two stages on the same tree.

Growth is distinctly cyclic and in some genera there are elaborate terminal buds and similar buds for pollen cones. Seed-bearing structures are usually produced on the latest shoots while pollen cones frequently emerge from shoots of the previous cycle. Sometimes leaves of only the last cycle persist on a tree but more common is the display of three or four cycles of growth.

Seeds germinate on or near the surface of the forest floor. The cotyledons remain at least partly inside the seed coat absorbing nourishment from the endosperm while the radicle penetrates the soil and begins forming a root system. Eventually the linear cotyledons shed the emptied seed coat and persist at the base of the growing shoot for a variable length of time. When functioning leaves are established, the cotyledons will be shed. Even if the adult leaves have some other form, the first foliage leaves in almost all taxa are bifacially flattened, often with an abrupt transition where the adult foliage is distinct.

Various parasites are known for this family. Members of *Podocarpaceae* are the exclusive hosts of three genera of fungus in the family *Coryneliales*, in Malesia recorded for *Podocarpus crassigemmis*. Their fruiting bodies can often be seen erupting from leaves or stems in *Podocarpus* or *Nageia*, but this does not seem to be particularly harmful. One species of *Korthalsella (Viscaceae)*, a dwarf mistletoe, is also parasitic in *Podocarpaceae*: *K. dacrydii* has been reported both on *Dacrycarpus* and on *Dacrydium* in various parts of Malesia (WASSCHER, Blumea 4, 1941, 320, 1 map).

Embryology. The fertilized egg undergoes four or five mitoses resulting in up to 16 to 32 free nuclei. Most of these are then walled off and cluster at the base of the archaegonium forming a pro-embryo of several tiers of cells. Those in the lowest tier are embryonic and divide to form binucleate cells of which there may be but one to in some genera as many as 16. The next tier of cells elongates into a 'prosuspensor' consisting of from 3 to 25 cells, the number of cells being roughly proportional to the size of the seed and therefore the length needed to reach the centre of the female gametophyte (later to become endosperm). A third tier of cells is not completely walled off and is left behind to degenerate as the embryonic mass is projected away. At the apex of the embryo there may be one or a few cells forming a 'cap'. Unless there are five mitoses (*i.e. Nageia* and *Prumnopitys* – both with large seeds) a larger number of suspensor cells means fewer embryonic cells. In the majority of cases the embryonic mass divides, along with the secondary suspensor which it generates, into several competing units, the common conifer condition known as cleavage polyembryony. Simple polyembryony resulting from more than one fertilized archaegonium also occurs. Growth of the embryo begins when the nuclei of the binucleate cells divide and then form groups of four cells. Probably an actual developed embryo derives from but a single binucleate cell so that, when there are more, they are competitive. The reduction of the number of embryonic cells often to a single cell in the genus *Podocarpus* appears to be a derived character. The binucleate embryo stage itself is unique in *Podocarpaceae*, while the number of mitoses leading to the pro-embryo is intermediate between a large number for *Araucariaceae* and non-coniferous Gymnosperms on the one hand and a smaller number for most other conifers on the other. *Sciadopitys* in the *Taxodiaceae* has five, while *Cephalotaxus* and most of the *Taxaceae* also have four.

Chromosomes. According to HAIR & BEUZENBERG (Nature 181, 1958, 1584) the chromosomes in *Podocarpaceae* are remarkable. Basically the number for the great majority is in effect n = 10 while for *Phyllocladus* it is n = 9 (and for *extra*-Mal. *Halocarpus* n = 8). For a great many species in most genera, however, there are two kinds of chromosomes. One type, always present, is median to submedian, while the other, sometimes present, is subterminal to subtelocentric. Two of the latter always correspond to one of the former indicating either a progressive splitting of some of the chromosomes or less likely a progressive pairwise fusion of some or all of the chromosomes. *Phyllocladus* and the genera with bilaterally flattened leaves (*Dacrycarpus, Falcatifolium*, and *Acmopyle*) have only the one kind of chromosome. The large genera *Dacrydium*, *Nageia*, and *Podocarpus* are partly with one kind and partly mixed. The other six (mostly small) genera always have mixed chromosome types. The result is a wide range of actual chromosome numbers from n = 8 to n = 19.

Occasionally hybrids have been noted or suspected. Many species occur side by side in nature without any apparent hybridization.

Taxonomy. Two recent works have treated all of what is recognized as a single family here. GAUSSEN (Les Gymnosperms actuelles et Fossiles, fasc. 13 & 14, 1974 & 1976) separates each of the three most distinct genera into families of their own, *viz. Saxegothaeaceae*, *Phyllocladaceae*, and *Pherosphaeraceae*. He recognizes one section of *Nageia* (*Afrocarpus*) as a distinct genus, while grouping the rest of this genus and *Parasitaxus* with *Podocarpus*. There are eight genera in *Podocarpaceae* as he envisions it. In my taxonomic revision (J. Arn. Arb. 50, 1969, 274–369) I recognize a single family and 13 genera (including the recently published *Halocarpus* by implication only).

Uses. The wood of trees in this family is light coloured, usually yellowish, is durable, easy to work, and generally similar to pine though rather harder. It is extensively used for lumber where sufficiently dense stands of good-sized trees occur, mostly outside of Malesia. In Borneo wood of *Nageia* is sometimes mixed with *Agathis* ('dammar') in commercial cuttings. Specimens of many genera are selected for planting around native settlements although the specimens seen in urban areas within Malesia usually come from China or Japan. In fact, natives in many areas so prize the wood for construction that, as I have been told on several occasions and have confirmed through experience, it is often necessary to go some distance from the nearest village to find mature wild trees. In some species the fruits are edible and I have found a few in tropical America that were locally appreciated but I have not discovered any such example in Malesia.

Note. Conifers lack flowers and even where brightly coloured fruit occurs it tends to be very transitory, thus conifers tend to be bypassed by collectors. Most genera are dioecious and separate collections of male and female are necessary. It is often desirable to have a juvenile specimen (low branches in the shade usually have the juvenile form) to appreciate the range of foliage form. Sometimes immense numbers of recently shed pollen cones are encountered on the forest floor and these are worth collecting.

VEGETATIVE KEY TO THE GENERA

1. Foliage in the form of 'cladodes' or flattened shoots .... **1. Phyllocladus**
1. Foliage of individual leaves.
 2. Foliage in the form of scales, needles, or linear leaves less than 2 mm wide.
  3. Foliage not dimorphic.
   4. Leaves not bilaterally flattened .... **2. Dacrydium**
   4. Leaves bilaterally flattened .... **3. Falcatifolium**
  3. Foliage dimorphic, leaves of ultimate branchlets longer and narrower than on main shoots may be bilaterally flattened .... **4. Dacrycarpus**
 2. Foliage in the form of broad flat leaves more than 2 mm wide.
  5. Leaves bilaterally flattened .... **3. Falcatifolium**
  5. Leaves bifacially flattened.
   6. Leaves with a groove over the midvein, (spirally placed,) lacking hypoderm, with a sweet taste **5. Prumnopitys**
   6. Leaves flat or with a ridge over the midvein, with hypoderm, without a sweet taste.
    7. Leaves opposite, many with multiveined leaves .... **6. Nageia**
    7. Leaves spirally placed, uninerved .... **7. Podocarpus**

GENERAL KEY TO THE GENERA

1. Foliage in the form of cladodes; several ovules erect within a leathery or fleshy cone . . **1. Phyllocladus**
1. Foliage of individual leaves; one to rarely several subterminal inverted seeds (ovules) projecting almost wholly beyond remainder of fertile structure.
 2. Inverted naked seed turning gradually as it matures to a nearly erect posture, cupped at the base by a thin epimatium, cone reduced to modified leaves which become fleshy when mature.
  3. Foliage as scales, needles, or small linear bifacially flattened leaves; fertile structure terminal on ordinary but sometimes short lateral foliage shoots .... **2. Dacrydium**
  3. Foliage as bilaterally flattened linear to oval-shaped leaves; fertile structure on a distinct scaly lateral shoot .... **3. Falcatifolium**
 2. Inverted seed enclosed by a leathery modified fertile scale, not turning, cone in most cases reduced to several scales, becoming fleshy or not.
  4. Leaves needles, scales, or small bilaterally flattened linear forms; fertile bract fused along one side of fruit, subtended by a small warty receptacle that becomes fleshy when mature ...... **4. Dacrycarpus**
  4. Leaves bifacially flattened; fertile bract separate from fruit, becoming fleshy or not.
   5. Fertile structure produced on a scaly (rarely leafy) shoot; covering of seed more or less fleshy.
    6. Leaves spirally placed, single veined, linear; seed nearly oval with slightly asymmetrical micropylar end, fertile axis never fleshy .... **5. Prumnopitys**
    6. Leaves opposite, often multiveined, oval; seed (usually) with a pronounced curving beak at the micropylar end, fertile axis in some cases a fleshy receptacle .... **6. Nageia**
   5. Fertile structure produced on a naked peduncle subtending a fleshy (or leathery) receptacle, covering of seed leathery (rarely somewhat fleshy) .... **7. Podocarpus**

1. PHYLLOCLADUS

L.C. RICH. *ex* MIRBEL, Mém. Mus. Hist. Nat. Paris 13 (1825) 76, *nom. cons.*; L.C. & A. RICH. Comm. Bot. Conif. & Cycad. (1826) 129, t. 3, f. 12; L.C. RICH. Ann. Sci. Nat. V, 20 (1874) 37; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 94, f. 18; Bot. Jahrb. 54 (1916) 33; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 249; DE LAUB. J. Arn. Arb. 50 (1969) 277; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 13, f. 675–9, map (f. 679bis); KENG, Ann. Bot. n.s. 26 (1962) 69, 14 fig.; Gard. Bull. Sing. 20 (1963) 123, 127; Ann. Bot. 38 (1974) 757; Taxon 24 (1975) 289; Pl. Syst. Ecol., Suppl. 1 (1977) 235; J. Arn. Arb. 59 (1978) 249, 43 fig., 4 maps; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 8. — *Podocarpus* LABILL. Nov. Holl. Pl. Sp. 2 (1806) 71, t. 221, *non* L'HÉRIT. *ex* PERS. (1807). — *Brownetera* L.C. RICH. Ann. Mus. Hist. Nat. Paris 16 (1810) 299, *nom. nud.* — *Thalamia* SPR. Anl. Kennt. Gewächse ed. 2, 2 (1817) 218. — **Fig. 6–8.**

Small to large trees up to 30 m tall, with smooth, dark, platy bark which is reddish or yellowish and fibrous within. Primary branches tend strongly to be in false whorls and secondary branching is abundant. The ultimate *foliar shoots* are flattened into cladodes or 'phylloclades' which involve a central axis and several alternate side 'shoots'. In outline these cladodes can be oval, triangular, deeply lobed, or compound and small marginal hooks representing reduced leaves can sometimes be seen. Shoots which are to continue growth, whether a secondary axis or a lobed cladode, terminate in a globular bud formed of overlapping triangular scales. These in turn develop into short shoots covered with linear lanceolate caducous scale-leaves in the axils of which new cladodes or fertile structures may be produced. Seedlings bear spirally arranged, single-veined, linear, acute bifacially flattened leaves up to 1 cm long followed gradually by smaller, more lanceolate forms until the adult scales are produced. Specimens are variously found to be dioecious or predominantly of one sex or fully monoecious. The cylindrical *pollen cones* are clustered each in the axil of a scale of a secondary shoot and are each subtended by a short to long, mostly naked stalk and by a few sterile scales. *Seed cones* appear singly or grouped either terminally or laterally in the axil of a scale on a naked stalk, at the base of a cladode, or terminally or laterally on a reduced or unreduced cladode. The cone consists of a few to many thickened spirally arranged scales, some of which bear a single erect ovule on the upper surface. The developing *seed* is surrounded to at least half its length by a symmetrical or nearly symmetrical filmy white aril or rough-edged epimatium. *Seeds* are oval and wider than thick, protrude from the bright red ripe cone, have a crooked micropyle at the tip, and are dark brown to black.

Distr. Five closely related species, three in New Zealand, one in Tasmania, and one in the highlands of *Malesia*. Fig. 5.

Fossils have been reported from the Eocene to Quaternary in New Zealand and from the Oligocene in New South Wales and Victoria (Australia); fossil pollen of Oligocene age was found in Australia, New Zealand and western Antarctica (COUPER, Proc. R. Soc. Lond. ser. B, 152, 1960, 491). The Malesian extension of the range was probably only reached in the late Tertiary. It is now extinct in Australia (FLORIN, Kongl. Svensk. Vet. Ak. Handl. III, 19, *n.* 2, 1940, 75, map 4; Acta Horti Berg. 20 (4), 1963, 184, t. 17: map).

Ecol. Upland tropical and temperate rain-forest, often mossy forest, as a large canopy tree to stunted forms near the tree line.

Note. The unique cladodes and fewer chromosomes set *Phyllocladus* apart from other *Podocarpaceae* but, as SINGH (Embryology of Gymnosperms, 1978, 257) points out, they share such common features as winged pollen with a prothallial tissue, an epimatium, and binucleate embryo cells. Other significant common traits are a solitary ovule per fertile bract, two pollen sacs per microsporophyll, and fused pairs of cotyledons as well as fleshiness of the mature cone and a mature seed of essentially identical form as those of other genera with naked seeds in the family. The erect seed with an aril has suggested a transitional position towards *Taxaceae* but the ovule is not terminal as in this group and the aril is not fleshy. FLORIN regarded the later developing aril as having nothing to do with the epimatium (Acta Horti Berg. 15, 1951, 267) but this position requires

Fig. 5. Range of the genus *Phyllocladus* L.C.RICH *ex* MIRBEL with the number of species.

Fig. 6. Branch with male cones of *Phyllocladus hypophyllus* HOOK.*f.* (Photogr. I. POLUNIN, 1978, received from H. KENG).

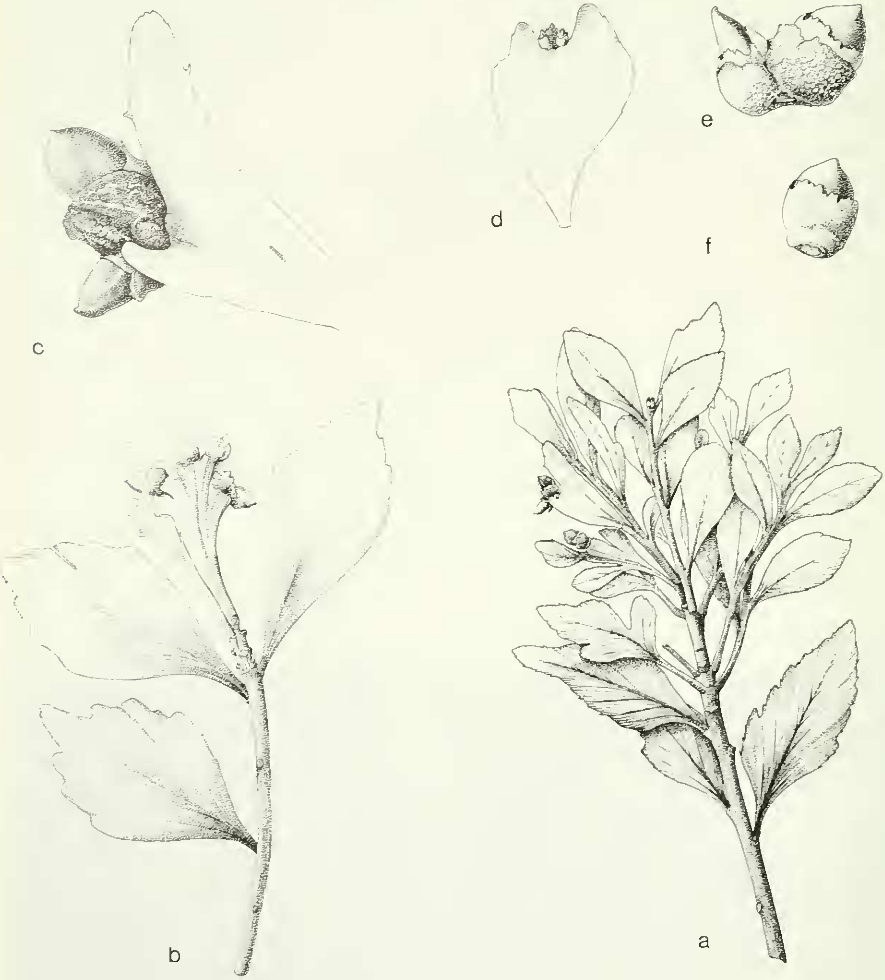

Fig. 7. *Phyllocladus hypophyllus* HOOK. *f.* a. Female shoot, ×0.5; b. ditto, ×0.5; c. ditto, ×2.5; d. cladode with immature female seed cones, ×1.5; e. seeds with bracts and epimatium, ×3; f. seed with epimatium, ×3 (*a* SAN 69968, *b–f* BELLAMY 1404).

the loss of any epimatium-type structure and the subsequent development of the morphologically similar (asymmetrical) aril in the corresponding location. In fact the erect position of the ovule may tend to suppress or delay the development of the epimatium which elsewhere arches over and around the base of inverted ovules. The only other genus of the family with an erect ovule has no epimatium at all while that of *Phyllocladus*, though eventually well developed, is retarded, appearing only after fertilization. The genus is a comfortable member of the *Podocarpaceae* and a distinct family, as KENG (Taxon 24, 1975, 289) proposed, does not seem justified. The intriguing thesis of KENG (Ann. Bot. 38, 1974, 757) that the cladodes probably represent a relic of ancient progymnosperm telomic branch systems seems hardly sustainable in the light of the above as well as the further fact that perfectly typical coniferous leaves are produced in the juvenile phase.

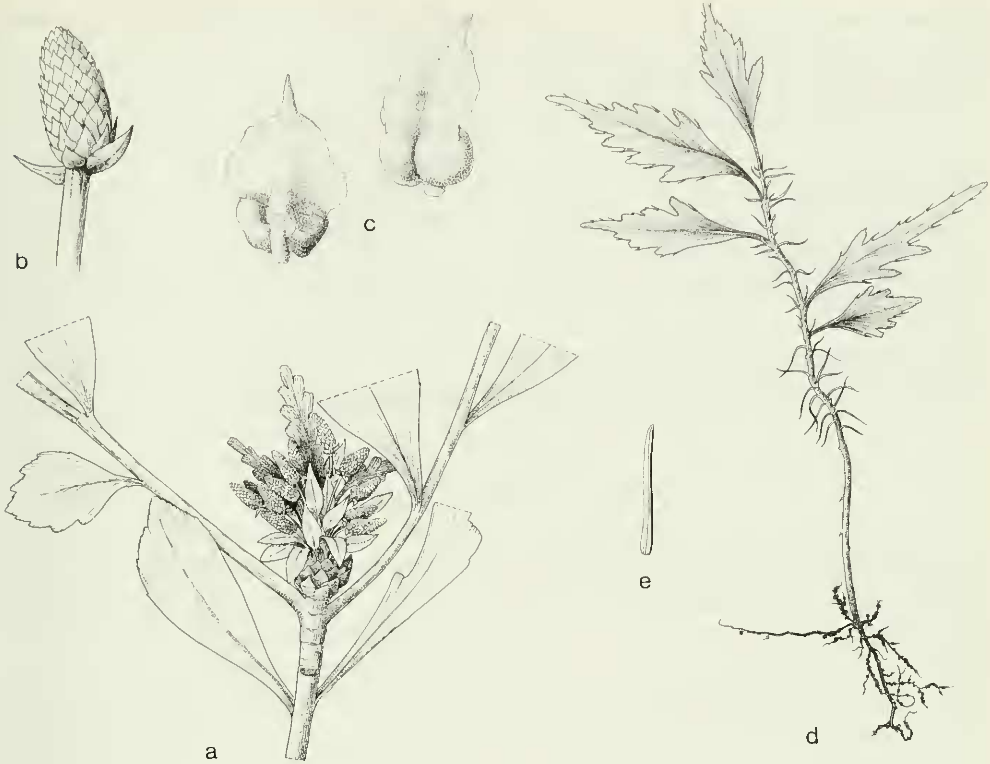

Fig. 8. *Phyllocladus hypophyllus* HOOK.*f.* a. Male shoot, ×1; b. male cone, ×3; c. microsporophylls (two views), ×6; d. old seedling, ×0.75; e. seedling leaf, ×3 (*a–c* DE LAUBENFELS P 636, *d–e* DE LAUBENFELS P645).

1. Phyllocladus hypophyllus HOOK.*f.* Icon. Pl. n.s. 5 (1852) t. 889; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 372; PARL. in DC. Prod. 16, 2 (1868) 499; STAPF, Trans. Linn. Soc. Bot. 4 (1894) 249; WARB. Monsunia 1 (1900) 194, *incl. var. protracta* WARB.; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 99; GIBBS, Contr. Phytogeogr. Arfak Mts (1917) 82; LANE-POOLE, For. Res. Papua & New Guinea (1925) 74; KENG, Gard. Bull. Sing. 20 (1963) 123, fig.; Ann. Bot. n.s. 27 (1963) 69, 14 figs., t. 1; DE LAUB. J. Arn. Arb. 50 (1969) 278, map 1; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 19 (1974) 17, f. 677 *p.p.*, f. 678; KENG, J. Arn. Arb. 59 (1978) 267, map 3; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 9, f. 34. — *P. protractus* (WARB.) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 99; FOXW. Philip J. Sc. 6 (1911) Bot. 165, t. 31; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 19 (1974) 17, f. 679. — *P. major* PILGER, Bot. Jahrb. 54 (1916) 211; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 19 (1974) 16, f. 677 *p.p.* — **Fig. 6–8.**

Large short-boled trees to shrubs near the tree line, up to at least 30 m tall. Bark dark brown to reddish, hard with large lenticels, light brown and granular within, breaking off in large, more or less rectangular scales. Foliar buds well developed, longer and less compact on younger plants, becoming more globular on older plants. *Juvenile leaves* 5–8 mm long and adult scale leaves 2–3 mm long. *Cladodes* on young plants deeply lobed and with distinct marginal hooks representing the reduced leaves, gradually becoming more compact, diamond-shaped to more or less oval with more or less wavy margins, 3–8 by 2–3 cm, the larger sizes mostly on young sterile specimens, marginal lobes *c.* 5 mm wide, often glaucous especially on the lower side, aggregated alternately on lateral branches of limited growth. *Pollen cones* usually produced on different plants than seed cones, each in the axil of a scale at the base of a growing shoot, in clusters up to 15, sometimes mixed with reduced cladodes, cylindrical, 12–15 mm long and 3 mm diameter with a naked peduncle 5–25 mm long. Apex of the microsporophyll triangular, irregularly toothed. *Seed cones* in an apical notch of a bilobed cladode or terminal on a reduced cladode or on a naked stalk *c.*

1 cm long, occasionally more than one together, ovoid and, like new cladodes, more or less purple, bearing up to 15 scales, of which usually 1–3 are fertile, becoming bright red when mature and then drying to a leathery brown. *Seed* shiny brown, 5–7 mm long.

Distr. *Malesia*: Philippines, Borneo, Celebes, Moluccas, New Guinea. Fig. 9.

Ecol. Moist mountain forests sometimes as low as 900 m up to tree line at 3200–4000 m. Scattered in the forest at lower elevation where trees may be quite large. More common but of reduced stature at higher elevations.

Note. The lower elevation occurrences are apparently examples of the phenomenon 'temporary settlement' from established higher elevation populations as described by VAN STEENIS in his Mountain Flora of Java (1972).

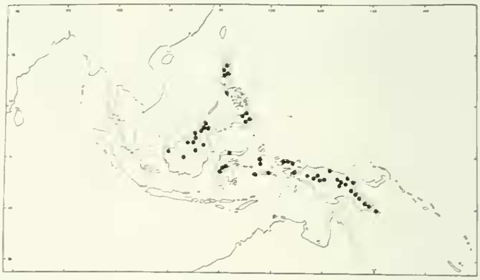

Fig. 9. Range of *Phyllocladus hypophyllus* HOOK.*f.*

2. DACRYDIUM

SOLANDER *ex* FORST.*f.* De Pl. Escul. Ins. Ocean. Austr. Comm. Bot. (1786) 80; Fl. Ins. Austr. Prod. (1786) 92; *ex* LAMBERT, Gen. Pinus ed. 1 (1807) App. 93, t. 41; RICH. Comm. Bot. Conif. & Cycad. (1826) 127; ENDL. Syn. Conif. (1847) 224; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 405; PARL. in DC. Prod. 16, 2 (1868) 493; BENTH. & HOOK.*f.* Gen. Pl. 3 (1880) 433; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 106; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 43, f. 4–6; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 239; FLORIN, Kongl. Svensk. Vet. Ak. Handl. 10 (1931) 248, f. 71; CORNER, Gard. Bull. S. S. 10 (1939) 239, t. 5–10; DE LAUB. J. Arn. Arb. 50 (1969) 282, f. 1–5; Fl. Nouv. Caléd. et Dép. 4 (1972) 17; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 11, f. 681–697, t. 85–87; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 33; QUINN, Austr. J. Bot. 30 (1982) 311. — *Lepidothamnus* PHIL. Linnaea 30 (1860) 730; QUINN, Austr. J. Bot. 30 (1982) 316, f. 7–8. — *Lagarostrobus* QUINN, Austr. J. Bot. 30 (1982) 316, f. 5–6. — **Fig. 14, 18, 19.**

Usually dioecious shrubs to large trees as much as 40 m tall. Bark hard and smooth with fissures and breaking off in plates, with numerous small lenticels, reddish brown and weathering to gray, slightly fibrous within. Profusely branched with the major side branches in many species curving gradually upward candelabra-like and the ultimate branches aggregated into dense tufts, others less formal or even drooping. The apex of a resting foliage shoot loosely covered by a cluster of short leaves or scales. *Leaves* spirally placed. Juvenile leaves awl-shaped, spreading sharply from a briefly decurrent base at about a 75° angle and the tip in nearly every species bent more or less forward in a gradual curve, lanceolate or linear-lanceolate, acute to apiculate, strongly keeled on the dorsal (abaxial) side and slightly or not at all on the axial side, roughly tetragonal to triangular in cross section, normally longer and occasionally more slender than the mature leaves. *Leaves on mature plants* more variable among the species, from small keeled adpressed scales 1 mm long to linear leaves or needles as much as 2 cm long, straight to strongly incurved at the tip, tetragonal in cross section or keeled on the dorsal side and flat or even strongly concave on the axial surface, in some cases as much as six times as wide as thick, apex blunt to narrowly acute. Where adult leaves differ sharply from the juvenile leaves the transition may be gradual or almost abrupt and juvenile shoots mixed with adult foliage are often seen. *Fertile structures* usually start with a few reduced leaves and are placed either terminally or laterally, often both, but in the species without lateral structures they may nevertheless be on short lateral branches. The cylindrical *pollen cones* may be solitary with a few reduced sterile leaves on a subtending axis or they may be clustered with one or more lateral cones in the axils of reduced leaves beside an often slightly larger terminal cone. Microsporophylls either with a triangular apex tapering from the pollen sacs or with a lanceolate apex sharply narrower than the pollen sacs. *Seed-bearing structure* with slightly enlarged scale-shaped bracts or with bracts resembling normal leaves and distinctly longer than the reduced leaves which they follow and more or less expanded at their base. The entire seed-bearing structure with the exception of the apical part of the bracts has been observed in the majority of species to become greatly enlarged, fleshy, and red when mature. In two middle latitude (New Zealand) species (the genus *Lagarostrobus* QUINN) the fertile bracts are not subterminal as in the remaining species, where usually one or in some species two or more may be fertile. The solitary ovule of a fertile bract is cupped by an epimatium which represents the fertile scale and which lies between the ovule and the subtending fertile bract. In a few species the ovule apex at pollination is only slightly inverted and faces inward towards the fertile axis, but in most species it is strongly inverted while in all species it gradually turns upward as the seed develops until it reaches a nearly upright position. *Seeds* become dark brown and have the same shape as those of *Phyllocladus*.

Distr. In all 25 *spp.*, from Southeast Asia through Malesia (not in Java and the Lesser Sunda Islands) to New Caledonia and Fiji, Tasmania, New Zealand and southern Chile. Within *Malesia* (14 *spp.*) the greatest variety is found in Borneo (7 *spp.*), followed by New Guinea (6) and Malaya (5), while both New Caledonia and New Zealand have 4 endemic species each. Fig. 10.

Fossils indicate that *Dacrydium* has a long fossil record, dating back to the Middle Jurassic and Upper Cretaceous floras of western Antarctica; in fact a centre of development was in the Australian–New Zealand–Antarctic region during the Upper Mesozoic. Obviously the centre of development was in the Australasian region. Its withdrawal from Australia did not take place before the Miocene (FLORIN, Kongl. Svensk. Vet. Ak. Handl. III, 19, *n.* 2, 1940, 74; Acta Horti Berg. 20 (4), 1963, 186, f. 18: map).

Taxon. The genus can be loosely divided into four subgroups (those with scale leaves, those with leaves much wider than thick, those with broadly triangular apices to the microsporophylls, and those with none of these characters) each of which is widely distributed in Malesia and somewhat beyond. The seemingly most primitive forms are concentrated in New Zealand with one in Tasmania.

Note. *Dacrydium* includes species whose leaves, progressing from acicular juvenile forms to mature scales, correspond to common early Mesozoic fossil foliage forms. Similar examples are also found in other families. A primitive clustering of pollen cones is found in the genus but the seed cones show an intermediate stage of development for the family. The most primitive seed cone form in *Dacrydium* is a rather loose structure with bracts resembling foliage leaves, rather than the compact cone of several other genera and of

Fig. 10. Range of the genus *Dacrydium* SOLANDER *ex* FORST.*f.* Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

preceding fossil conifers. Other seed-bearing structures are further reduced to fewer fertile units and an exposed subterminal seed placement anticipating the more formal structure in the more advanced genera of the family. The rotation of the seed as it matures is a specialized trait.

KEY TO THE SPECIES

1. Adult leaves in the form of imbricate scales [microsporophylls triangular].
  2. Mature seed completely exposed above short (to 2 mm) cone bracts; juvenile leaves nearly straight, up to twice as wide as thick; adult scales appearing gradually on trees several meters high . **1. D. elatum**
  2. Mature seed base overlapped by elongated (3 mm) cone bracts; juvenile leaves strongly bent forward and slightly inward, about three times as wide as thick, adult scales appearing almost abruptly on small specimens about half a metre high . . . . **2. D. novo-guineense**
1. Adult leaves spreading linear or lanceolate needles or leaves.
  3. Microsporophylls triangular; female terminal (occasionally on short lateral branches); leaves bent forward, up to 5 mm long and length about 5 times width.
    4. Leaves blunt (may be apiculate), width less than twice thickness.
      5. Mature seed fully exposed above short cone bracts [leaves robust (0.3–0.4 mm thick)] **3. D. pectinatum**
      5. Mature seed barely overtopping elongated cone bracts.
        6. Leaves spreading their tips bent parallel to the branch or directed outward, blunt or with a small apiculus, becoming triangular in cross section and about as thick as wide, 0.2–0.3 mm thick **4. D. nidulum**
        6. Leaves crowded and more or less touching near their tips which on mature plants curve inward towards the branch, distinctly apiculate, nearly twice as wide as thick, 0.3–0.4 mm thick **5. D. cornwalliana**
    4. Leaves acute, width more than twice thickness . . . . **1. D. elatum** (occasional specimens)
  3. Microsporophylls sharply narrowed above the pollen sacs and lanceolate; female may be lateral in some species; leaves acute, in many species to more than 5 mm long and length generally at least 8 times width.
    7. Leaves triangular in cross section, width no more than three times thickness.
      8. Leaves spreading (nearly straight), 0.3–0.4 mm wide, less than twice thickness, length about 25 times width . . . . **6. D. beccarii**

8. Leaves bent forward, 0.4–0.6 mm wide and width 2–3 times thickness, length no more than 12 times width.
9. Leaves mostly 0.4 mm wide; male 6–7 mm long; microsporophyll barely 1 mm long; mature seed exposed .... **7. D. gracilis**
9. Leaves up to 0.6 mm wide; male more than 7 mm long; microsporophyll 1.5–2 mm long; mature seed partly covered by elongated cone bracts.
10. Leaves slightly bent forward, length up to 10 times width; male 7–9 mm long ... **8. D. medium**
10. Leaves strongly bent forward, length more than 10 times width; male about 12 mm long **9. D. magnum**
7. Leaves distinctly concave on the underside or wide and flat, width at least 8 times thickness.
11. Leaves at least 3 mm long.
12. Female terminal, bracts about as long as leaves, mature seed partly covered; leaves up to 7 mm long, apex abrupt and bent forward.
13. Leaves 3–5 mm long, only slightly bent (male unknown) .... **10. D. spathoides**
13. Leaves 5–7 mm long, strongly bent; microsporophyll very long (5–6 mm) ..... **11. D. gibbsiae**
12. Female mostly lateral, bracts much smaller than leaves, mature seed exposed; leaves at least 6 mm long.
14. Leaves slightly bent forward and concave, lanceolate, narrowly acute.
15. Leaves 6–10 mm long, 0.5–0.8 mm wide. .... **12. D. xanthandrum**
15. Leaves at least 10 mm long, 0.7–1.3 mm wide .... **13. D. comosum**
14. Leaves straight and flat, linear, more or less abrupt at the apex, up to 10 mm long **14. D. ericoides**
11. Leaf about 1 mm long, strongly bent forward .... **15. D. leptophyllum**

1. Dacrydium elatum (ROXB.) WALL. *ex* HOOK. London J. Bot. 2 (1843) 144, t. 2; ENDL. Syn. Conif. (1847) 226; BLUME, Rumphia 3 (1849) 221, t. 172B, f. 1 & 172C, f. 2; MIQ. Fl. Ind. Bat. 2 (1859) 1075; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 406; DE BOER, Conif. Arch. Ind. (1866) 29; PARL. in DC. Prod. 16, 2 (1868) 494; HOOK.*f.* Fl. Br. India 5 (1896) 648; RENDLE, J. Bot. 34 (1896) 355; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 51; RIDLEY, J. Str. Br. R. As. Soc. *n.* 60 (1911) 55; Fl. Mal. Pen. 5 (1925) 279, f. 227; BURKILL & HOLTTUM, Gard. Bull. S. S. 3 (1923) 75; CORNER, Gard. Bull. S. S. 10 (1939) 240, t. 5; Wayside Trees (1940) 721, t. 223–224; DE LAUB. J. Arn. Arb. 50 (1969) 285; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1d; PHENGKLAI, Thai For. Bull. 7 (1973) 9, f. 5; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 48, f. 692, t. 86. — *Juniperus elata* ROXB. Fl. Ind. 3 (1832) 838. — *D. junghuhnii* MIQ. Pl. Jungh. 1 (1851) 4; Fl. Ind. Bat. 2 (1859) 1075. — *D. pierrii* HICKEL, Bull. Soc. Dendr. France 76 (1930) 74; Fl. Gén. I.-C. 5 (1931) 1070, f. 123, 2–4; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 46, f. 691, t. 87. — *D. beccarii var. subelatum* CORNER, Gard. Bull. S. S. 10 (1939) 243, t. 7; DE LAUB. J. Arn. Arb. 50 (1969) 303; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1c.

Large tree, 8–40 m high, 0.1–1 m diam., with many slender, more or less erect branches and crowds of branchlets forming tufts which together construct a great billowy dome. *Juvenile leaves* linear-lanceolate, pungent, spreading but curved forward parallel to the branch, keeled on four sides, to at least 14 mm long, 0.3 mm wide and 0.2 mm thick, gradually becoming shorter and slightly broader with the leaves at the bases of ultimate shoots and on more vigorous shoots noticeably smaller and less spreading. Transitional forms which are sometimes fertile have spreading leaves slightly bent forward towards the acute tip, triangular in cross section, 0.3–0.4 mm wide, 0.2 mm thick, and 2–4 mm long, the leaves on vigorous shoots more nearly scale-like. *Adult foliage shoots* cord-like, 1–2 mm diam., leaves in the form of imbricate triangular scales 1–1.5 by 0.4–0.6 mm, sharply keeled on their exposed surface. Juvenile shoots sometimes mix with adult shoots thus giving a false impression that leaves change abruptly as the tree matures. The fertile structures are terminal. *Pollen cones* small, 4–5 mm long and 1–1.2 mm in diam. Apex of microsporophyll 0.5–0.8 mm long. The *seed-bearing structure*, even when produced on needle-bearing branches, is subtended by a scaly peduncle several mm long with scales about 1 mm long. The seed cone consists of about a dozen slightly elongated bracts 1.5–2 mm long. The solitary *seed* is 4–4.5 mm long.

Distr. Indochina and Thailand; in *Malesia*: Malaya (very common, incl. Penang I.), Sumatra (only local in Westcoast Res., Batak Lands), Borneo (Sarawak, Sabah, rather rare). Fig. 11.

Ecol. Scattered in moist rain-forest, from sea-level but mostly above several hundred m to 1,700 m, growing most abundantly in open situations indicating a preference for disturbed conditions. It also appears to prosper on difficult soils (sandstone, granite, kerangas). Hardy and popular under cultivation in fully exposed sites. Does not enter into high mountain scrub.

Vern. *Ru*, M (properly the common name for

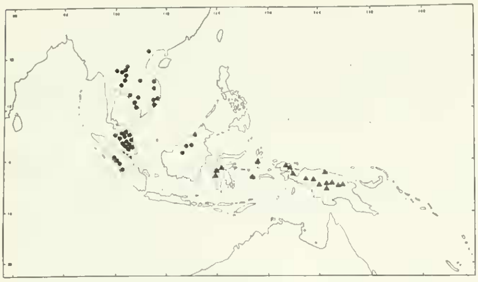

Fig. 11. Range of *Dacrydium elatum* (ROXB.) WALL. *ex* HOOK. (dots) and *D. novo-guineense* GIBBS. (triangles).

Gymnostoma (Casuarinaceae); Borneo: *ouk*, Kayan, *sempilor*, Merurong Plateau.

Note. *Dacrydium beccarii var. subelatum* was established for trees bearing the intermediate foliage, a condition which appears to be persistent on certain individuals, some of them growing on high mossy ridges. Actually fruiting specimens with intermediate foliage occur sporadically throughout the range of *D. elatum* (DE LAUBENFELS, Blumea 23, 1976, 97). CORNER thought that this variety was somehow transitional, even suggesting that *D. beccarii* — of which he made it a part — might be a hybrid between *D. comosum* and *D. elatum*. Indeed, the individuals on high mossy ridges may well be hybrids between *D. beccarii* and *D. elatum* as they seem always to occur where the ranges of these two species approach one another. In any case, all such plants can be distinguished by much shorter leaves on vigorous shoots than for *D. beccarii* and generally variable leaf size.

2. Dacrydium novo-guineense GIBBS, Contr. Phytogeogr. Arfak Mts (1917) 78, f. 3; DE LAUB. J. Arn. Arb. 50 (1969) 286; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 44, f. 693.

Tree, 1.5–29 m tall, up to 50 cm diam., with ascending branches and numerous branchlets producing a dense rounded crown. *Juvenile leaves* up to at least 1 cm long, lanceolate, acute, spreading but curved so that the apex normally turns slightly inward towards the shoot, often shorter at the base of the shoot and on main axes, strongly keeled on the back, 0.2 mm thick and 0.4–0.7 mm wide, giving way abruptly to short transitional scales on plants about half a metre high, sometimes twisted to the side giving a spiral effect to the shoot. *Transitional leaves*, if present, up to *c.* 2 mm long and spreading slightly. *Adult shoots* cord-like, 1–2 mm diam. Adult scale-leaves strongly keeled on the back, acute, imbricate, 0.8–1.7 mm long and 0.4–1 mm wide. *Fertile structures* terminal, usually on short or very short lateral shoots. *Pollen cones* 5–8 mm long and 1.5 mm diam., apex of the microsporophyll less than 1 mm long. *Seed-bearing structure* formed of elongated bracts, the longest towards the apex 3 by 0.5 mm. *Seed* 5 mm long and dark brown.

Distr. *Malesia*: Central & SE. Celebes, Moluccas (Buru, Obi), and throughout New Guinea. Fig. 11.

Ecol. Along mossy crests and in open areas from 700 to 3000 m, but mostly between 1500 and 2200 m. Rising above the mid mountain canopy or a common small tree at higher elevations rising above ferns and other scrub often after fire, sometimes dominant. On different soil types: clay, stony sand, quartzite, even peat. Very common in New Guinea.

Vern. New Guinea: *kaowié*, *kowié*, Arfak, Manikiong lang., *aru*, Wissel Lakes, Kapauko lang., *munump*, Nondugl, Minj.

Note. Other scale-leaved species of *Dacrydium* occur in the Antarctic forests of Tasmania, New Zealand, and Chile. *Dacrydium novo-guineense* is a tropical highland tree while, among the scale-leaved group in *Dacrydium*, only *D. elatum* occurs in tropical lowlands.

3. Dacrydium pectinatum DE LAUB. J. Arn. Arb. 50 (1969) 289, f. 1b–2; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 42, f. 689; DE LAUB. Kalikasan 7 (1978) 121. — *D. pectinatum var. robustum* DE LAUB. J. Arn. Arb. 50 (1969) 291, f. 1c.

Small to large tree, 3 to 40 m tall, with numerous branchlets forming a dense rounded crown. *Juvenile leaves* up to 18 mm long, slightly curved, pungent, strongly keeled and quadrangular in cross section, 0.2 mm wide and thick, gradually becoming shorter and thicker. *Adult leaves* keeled on four sides but less strongly on the axial side, abruptly acute to blunt, slightly curved, 2–5 by 0.4–0.8 mm wide and thick. *Fertile structures* terminal. *Pollen cone* 6–12 mm long and 2 mm diam., apex of microsporophyll 1–1.2 mm long. The *seed-bearing structure* subtended by a short zone of small leaves *c.* 2 mm long while the cone bracts themselves may be up to 3 mm long. *Seed* 4–4.5 mm long.

Distr. Hainan; in *Malesia*: Billiton, Borneo (incl. Karimata & Natuna Is.) and Philippines (Lu-

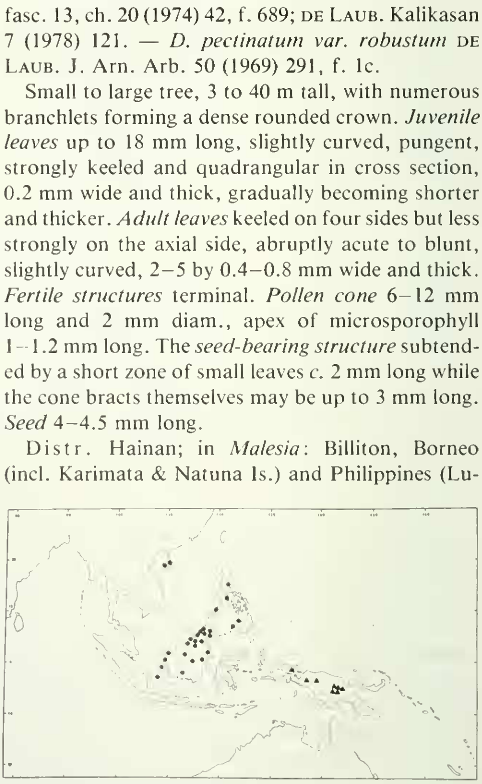

Fig. 12. Range of *Dacrydium pectinatum* DE LAUB. (dots) and *D. cornwalliana* DE LAUB. (triangles).

zon: Sierra Madre; Mindanao: Zamboanga, 2 coll.), in Borneo common. Fig. 12.

Ecol. Scattered large individuals are found in primary rain-forest other than dipterocarp forest from sea-level to 1500 m but mostly below 600 m, while dense stands are found in boggy areas and nearly pure stands of stunted trees occur in shallow sandy soils, especially on so-called 'padangs', and on kerangas in heath forest, frequently associated with *Gymnostoma*; in Sabah also on ultrabasic soils. In Kayangeran For. Res. (Brunei) reported to occur in pure stands in the centre of peat swamps.

Vern. *Mélo*, Natuna; Borneo: *malur*, Mangar, *melur*, Singkawang, *tjemantan*, Sampit, *sempilor*, Sarawak, Sabah.

Note. This species closely resembles the lowland form of *D. nidulum* from which it differs by the more robust leaves and by the fully exposed mature seed. *Dacrydium balansae* in New Caledonia and *D. cupressinum* in New Zealand are also similar. The variety was created for markedly shorter leaves, a condition which, it turns out, is related to more difficult environments and all variations can be seen in local populations across environmental gradients.

4. Dacrydium nidulum DE LAUB. J. Arn. Arb. 50 (1969) 292, f. 3a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 42, f. 688.

Tree 10 to 30 m tall, 18–50 cm diam., with numerous branchlets forming a dense crown. *Juvenile leaves* up to 2 cm long, slightly curved forward, acute, triangular in cross section, 0.2 mm wide and less thick. *Adult leaves* not crowded (leaf tips distant from adjacent leaves), nearly straight to distinctly curved so that the apex is parallel with the shoot, abruptly acute to blunt, often apiculate, 1–5 mm long but mostly 2–3.5 mm, triangular in cross section, strongly keeled on the back, 0.3–0.7 mm wide and 0.2–0.3 mm thick. *Fertile structures* terminal but pollen cones may also be lateral. *Pollen cones* 8–18 mm long and 1–1.6 mm diam. Microsporophylls 0.8–1.2 mm long. *Seed-bearing structure* subtended by leaves distinctly shorter than normal foliage leaves, as short as 1.5 mm; cone bracts increasing towards the apex where one or two may be fertile, up to 4 mm long and completely surrounding the epimatium but surpassed by the apex of the mature *seed* which is 3.5–4 mm long and glossy brown.

Distr. W. Polynesia (Fiji); in *Malesia*: throughout New Guinea (incl. Normanby & Japen Is.) to the Moluccas (Halmaheira) and Central & SE. Celebes and the Lesser Sunda Islands (Sumba). Common in the western parts of New Guinea, but elsewhere populations are mostly rather isolated. Fig. 13.

Ecol. A canopy tree of primary and sometimes secondary rain-forest from sea-level to 1200 m but mostly under 600 m.

Vern. New Guinea: *chawènum, kasuari, kwennum*, Arfak, Maibrat lang., *tjikwal*, Hattam lang., *jammari*, Wandammen, *samiampi*, Japen, Roberbai dial., *kun*, Eipomek valley, Irian, *ibaro*, Upper Waria, *binban*, Oriomo, *nidjon*, Kebar valley, *nipaj*, Karoon lang., Arfak, *uier*, west of Hollandia, Itik lang.

Note. There is some variation between the different widely distributed populations. In the Cycloop

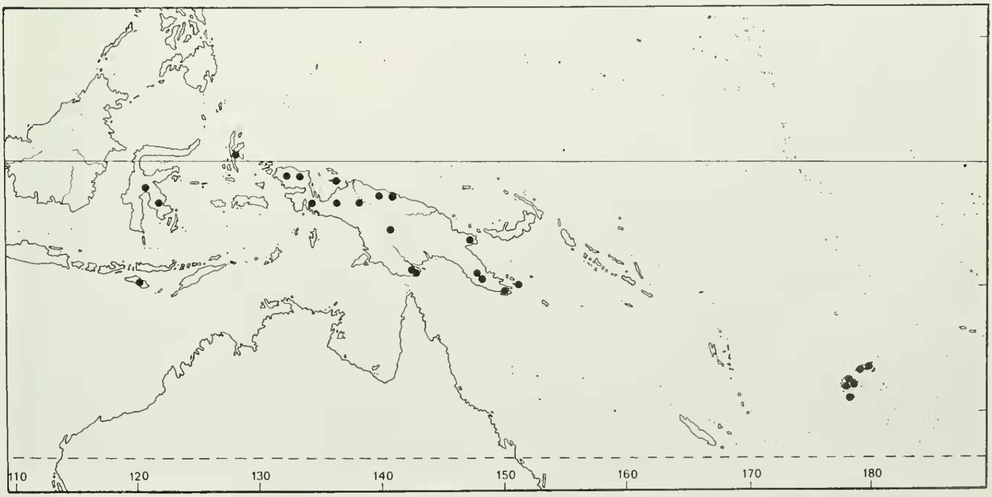

Fig. 13. Range of *Dacrydium nidulum* DE LAUB.

Mts and in Fiji the leaves are not apiculate and, particularly in Fiji, the leaves are nearly straight. Variations in length seem to be mainly a function of age or exposure, with younger and protected plants tending to have longer leaves.

5. Dacrydium cornwalliana DE LAUB., *nov. sp.* — *D. nidulum var. araucarioides* DE LAUB. J. Arn. Arb. 50 (1969) 295, f. 36. — **Fig. 14.**

Arbor ad 30 m alta. Folia conferta, apicum tangentum incurvum apiculatum, latiora quam crassa, 0.3–0.4 mm crassa. Type: VERSTEEGH BW 3041 (L, holo), Wissel Lakes, West Irian.

Tree 10–30 m tall, with elongated dense fastigiate crown. *Juvenile leaves* up to 12 mm long, strongly curved forward parallel to the branch and soon becoming incurved, 0.4–0.5 mm wide and 0.2–0.3 mm thick, sharply apiculate. *Adult leaves* crowded and touching near their tips, spreading but then incurved towards the tip which is directed somewhat inward towards the branch, distinctly apiculate, 2–5 mm long, the longer examples on protected branches or younger trees, strongly keeled on the back and slightly concave on the ventral side but with a small ridge over the midvein, 0.6–0.8 mm wide and 0.3–0.4 mm thick. *Fertile structures* terminal, often on short lateral shoots but pollen cones may also be lateral. *Pollen cones c.* 12 mm long and 1.8 mm in diam. Microsporophylls *c.* 0.8 mm long. *Seed-bearing structure* as in *D. nidulum*, becoming fleshy and red when ripe, *seed c.* 5 mm long.

Distr. *Malesia*: West and Central New Guinea. Fig. 12.

Ecol. Dominant to nearly pure stands in swamp forests and perhaps also mossy heath forests between 1450 and 2300 m altitude.

6. Dacrydium beccarii PARL. in DC. Prod. 16, 2 (1868) 494; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 52; RIDLEY, J. Str. Br. R. As. Soc. *n.* 60 (1911) 56; BURKILL & HOLTTUM, Gard. Bull. S. S. 3 (1923) 75; RIDLEY, Fl. Mal. Pen. 5 (1925) 280; CORNER, Gard. Bull. S. S. 10 (1939) 241, t. 6; Wayside Trees (1940) 720; DE LAUB. J. Arn. Arb. 50 (1969) 300; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 38, f. 682 *p.p.*; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 34.

Shrub of 1 m or a small tree up to 20 m, rarely to

Fig. 14. *Dacrydium cornwalliana* DE LAUB., edge of forest on black peat; in the background mixed forest with amongst others *Libocedrus*. Wissel Lakes, New Guinea, 1700 m (Photogr. F.W.RAPPARD, 1955).

35 m tall. Profusely branched with the branches turned upward, often forming a dense umbrella- or dome-shaped crown. *Juvenile leaves* nearly straight at first on fresh growth, becoming gradually curved forward, up to 17 mm long, strongly keeled on three sides, nearly flat on the axial surface, 0.2 mm wide and 0.1 mm thick, linear-lanceolate, pungent, crowded so that shoots resemble a furry animal's tail. *Adult leaves* spreading, bent slightly forward but the apiculate tips still directed slightly outward, triangular in cross section, 0.3–0.4 mm wide, 0.2 mm thick, crowded, linear-lanceolate, 5–10 mm. *Fertile structures* both lateral and terminal. *Pollen cones* subtended by a cluster of sterile 1–2 mm bracts, the cone 7–10 mm long and 2.5–3 mm diam. Apex of the microsporophyll a lanceolate spur about 1 mm long and 0.3 mm wide at the base. *Seed-bearing structure* subtended by about a dozen reduced leaves *c.* 1 mm long, the seed cone itself formed of a similar number of bracts up to 2 mm long and not completely covering the epimatium, often two and occasionally even three seeds which are fully exposed at the apex of the structure. *Seeds* shiny, dark brown, *c.* 4 mm long.

Distr. Solomon Islands (Guadalcanal); through *Malesia*: New Guinea (incl. Normanby I. & New Britain), the Moluccas (Taliabu), Philippines (Mindanao; Negros; Biliran I.) and (mainly W.) Borneo to Malaya and N. Sumatra. In the eastern part of the range there are only widely separated occurrences, and even in the western part they are somewhat discontinuous. Fig. 15.

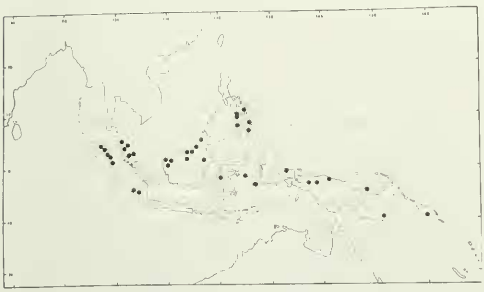

Fig. 15. Range of *Dacrydium beccarii* PARL.

Ecol. Most common on mossy ridges where it is often dominant and also found rising above a low mixed mountain scrub, from 600–2500 m. A variety of soils such as sandy peat and andesite have been indicated.

Vern. New Guinea: *netukuria*, New Britain, *mejoop*, Kebar valley; Taliabu: *kawau*; Borneo: *kayu embun*, Merurong Plateau, *sempilor*, Sarawak, Bintulu; Malaya: *ekor kuda*, Kedah; Sumatra: *sampinur tali*, Tapanuli.

7. Dacrydium gracilis DE LAUB., *nov. sp.*

Arbor ad 30 m alta. Folia linearia lanceolata, dorsis carinatis, apices apiculatis, 3–9 mm longa, 0.4 mm lata, 0.2 mm crassa. Strobili masculi 6–7 mm longi, 2 mm diametri. Apices microsporophyllorum lanceolati, 0.5–1 mm longi, c. 0.3 mm lati. Semina matura non obscurata. Type: DE LAUBENFELS P716 (L, holo), Mt Kinabalu.

Tree 7–30 m tall, up to 40 cm diam. *Juvenile leaves* at least 12 mm long, curved so that the tip is nearly parallel to the branch, pungent, triangular in cross section, lanceolate, up to 0.4 mm wide, at the base 0.2 mm thick. *Adult leaves* nearly straight, spreading at about a 45° angle but curved so the apex is parallel with the branch, apiculate, 3–9 mm long, the longer leaves on younger plants or lower on the tree, the shorter leaves on older and exposed trees, triangular in cross section, 0.4 mm wide, 0.2 mm thick. *Fertile structures* usually lateral. *Pollen cones* 6–7 mm long and 2 mm in diam., subtended by a cluster of leaves 3–5 mm long and usually distinctly shorter than normal foliage leaves. Together the two pollen sacs are 0.7–0.8 mm wide but the apex of the microsporophyll is a lanceolate spur 0.5–1 mm long and *c.* 0.3 mm wide. *Seed-bearing structure* also subtended by a cluster of reduced leaves *c.* 1 mm long, the bracts of the seed cone up to 3 mm long and more or less covering the epimatium, the usually solitary seed itself fully exposed. Fully mature seeds unknown.

Distr. *Malesia*: Borneo (Sabah: Mt Kinabalu and nearby to the centre of Borneo; Sarawak). Fig. 16.

Fig. 16. Range of *Dacrydium gracilis* DE LAUB. (triangles) and *D. spathoides* DE LAUB. (dot).

Ecol. Scattered in the canopy of moist mountain rain-forest between 950 and 1800 m, in Sarawak also in heath forest on sandstone. Rather rare.

Note. Leaves smaller and much more gracile than those of the similar *D. magnum* which also occurs in lower elevation forest. The crown has a rather typical shape of a forest tree, not the striking form of the usually open growth species, *D. beccarii*.

8. Dacrydium medium DE LAUB. Blumea 23 (1976) 98.

Shrub of 1 m or a small, often gnarled tree, sometimes up to 20 m tall. Densely branched to form a compact oval shape. *Juvenile leaves* spreading widely but sometimes distinctly curved forward so that the apiculate apex is more or less parallel to the branch, lanceolate, up to 20 mm long, strongly keeled on three sides, nearly flat on the axial surface, up to 0.6 mm wide, 0.3 mm thick. *Adult leaves* on younger trees nearly straight and up to 8 mm long but with greater age the leaves become shorter and sharply curved forward or even slightly inward, apiculate, linear-lanceolate, 3–6 mm long but nearly uniform on a branch, 0.5–0.6 mm wide, 0.3 mm thick. *Fertile structures* mostly terminal. *Pollen cones* with basal leaves hardly different from foliage leaves, 7–9 mm long, 2.5 mm diam. Apex of the microsporophyll a linear-lanceolate spur 1.5–2 by 0.5 mm with the broadly acute apex strongly curved inwards so as to appear rounded and blunt. *Seed-bearing structure* subtended by a zone of reduced leaves about 2 mm long, the cone bracts longer and partly covering the seed. The brown seeds about 5 mm long.

Distr. *Malesia*: Malaya (G. Tahan complex) and N. Sumatra (Gajo Lands: G. Leuser & Bandahara). Fig. 17.

Fig. 17. Range of *Dacrydium medium* DE LAUB. (dots) and *D. magnum* DE LAUB. (triangles).

Ecol. Rising above and often dominant in low mountain scrub on what appears to be rather poor soils between 960 and 2100 m in Malaya and 1800–2600 m in Sumatra; not rarely associated with *Baeckea* and *Leptospermum*.

Vern. *Sangu*, Gajo.

Note. The shortest leaved specimens resemble *D. pectinatum* foliage, a species which grows under similar conditions at lower elevations, but the fertile material more closely resembles several other species.

9. Dacrydium magnum DE LAUB. J. Arn. Arb. 50 (1969) 299, f. 4a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 36, f. 681 *p.p.* — *D. beccarii var. rudens* DE LAUB. J. Arn. Arb. 50 (1969) 303, f. 4b; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 38, f. 682 *p.p.*

Tree, 8–30 m tall, 5–60 cm diam. Branches dense, spreading, upturned. *Juvenile leaves* spreading widely, slightly curved forward at the tip, pungent, triangular in cross section, gracile, up to at least 18 mm long. *Adult leaves* spreading at about a 45° angle and strongly curved forward so that the apiculate tip is parallel to the branch or bent slightly inward, forming a compact rope-like branch system, linear-lanceolate, 3–6 mm long but nearly uniform on a branch, 0.3–0.4 by 0.2–0.3 mm. *Fertile structures* mostly terminal but occasionally on short lateral branches, the subtending leaves hardly distinguishable from ordinary foliage leaves. *Pollen cones* 10–16 mm long and 2 mm in diameter. Apex of the microsporophyll a lanceolate spur 1.5–2 mm long and 0.5 mm wide at the base. *Seed-bearing structure* formed of more or less straight and slightly spreading leaf-like bracts which cover the base of the seed. The ripe *fruit* reported to be brown but possibly an old fruit as has been observed in other species. *Seed* 5 mm long, often two seeds per cone.

Distr. Solomon Islands (Guadalcanal, Choiseul, S. Ysabel); in *Malesia*: Louisiades (Sudest I.) and Moluccas (Obi I.). Rare. Fig. 17.

Ecol. Locally common in the canopy of moist tropical forest between 60 and 1200 m, often along ridge crests where it has a somewhat reduced stature.

Note. The variety *rudens* was applied to collections from Tagula I. that tend to be more gracile than elsewhere but otherwise are not distinct.

10. Dacrydium spathoides DE LAUB. J. Arn. Arb. 50 (1969) 299, f. 3c; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 44, f. 690.

Tree 26–34 m tall, 50 cm diam. Bark exuding red sap. *Juvenile leaves* spreading at about a 60° angle, nearly straight but slightly bent forward at the pungent tip, to at least 6 mm long, linear-lanceolate, *c.* 1 mm wide, 0.2 mm thick, keeled on the dorsal side, slightly concave on the axial side. *Adult leaves* spreading at about a 45° angle, straight or slightly bent forward at the apiculate tip, 2–4 mm long, linear-lanceolate, 0.8–0.9 mm wide, 0.2 mm thick, keeled on the dorsal side, distinctly concave on the axial side. *Pollen cones* unknown. *Seed-bearing structure* terminal, often on a short side branch, subtended by reduced leaves less than 2 mm long, the cone bracts straight, slightly spreading, up to 3 mm long and 0.5 mm wide, covering the lower part of the seed. Mature *seed* 4 mm long, often two seeds per cone.

Distr. *Malesia*: Eastern West Irian. Fig. 16.

Ecol. Canopy tree in moist, mossy mountain rain-forest at 2150–2200 m.

11. Dacrydium gibbsiae STAPF, J. Linn. Soc. Bot. 42 (1914) 192, t. 4; DE LAUB. J. Arn. Arb. 50 (1969) 306; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 34, f. 681 *p.p.* — *D. beccarii var. kinabaluense* CORNER, Gard. Bull. S. S. 10 (1939) 244, t. 9. — *D. sp.* STAPF, Trans. Linn. Soc. II, 4 (1894) 248.

Small tree, 2–12 m tall. *Juvenile leaves* spreading widely, slightly curved forward towards the apiculate tip, at least 12 mm long, slightly wider than thick. *Adult leaves* robust, the acute tip bent to be parallel to the branch or even curved slightly inward, crowded, linear or linear-lanceolate, 5–8 mm long, concave on the axial side, strongly keeled on the dorsal side, 0.8 to at least 1 mm wide, 0.2–0.3 mm thick. *Fertile structures* terminal, often on a short lateral branch. *Pollen cones* 20–25 mm long and 4.5–7 mm diam.; microsporophyll lanceolate, 5–6 mm long, 1.5 mm wide at the base. *Seed-bearing structure* consisting of bracts slightly narrower than ordinary foliage leaves and increasing slightly in length towards the apex where one or two may be fertile, spreading slightly and completely covering the epimatium but surpassed by the apex of the mature *seed* which is 4.5 mm long.

Distr. *Malesia*: N. Borneo (Mt Kinabalu). Common on the slopes.

Ecol. Co-dominant un ultrabasic soils in the mountain mossy forest from 1500–3600 m.

12. Dacrydium xanthandrum PILGER, Bot. Jahrb. 69 (1938) 252; DE LAUB. J. Arn. Arb. 50 (1969) 304, f. 5; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 34, f. 683. — **Fig. 18, 19.**

Shrub to tree, 2–36 m tall, up to 70 cm diam. *Juvenile leaves* spreading widely, bent slightly forward, linear-lanceolate, up to 2 cm long, 0.8 mm wide, strongly keeled on the dorsal side, slightly keeled and slightly convex on the axial side, about 0.2 mm thick, apiculate. *Adult leaves* spreading widely, straight or slightly bent forward but the tips still directed outwards, lanceolate to linear-lanceolate, 6–10 mm long or shorter at the base of the shoot, apiculate, strongly keeled on the dorsal side, slightly keeled and slightly concave on the axial side, 0.5–0.8 mm wide, 0.2 mm thick. *Fertile structures* both terminal and lateral. *Pollen cone* subtended by a cluster of reduced leaves which are *c.* 2 mm long, cone 5–13 mm long and 2–2.5 mm diam.; apex of the microsporophyll a lanceolate spur 0.6–1.2 mm long and 0.3 mm wide at the base. *Seed-bearing structure* subtended by a shoot up to 4 mm long with reduced leaves *c.* 2 mm long or when terminal sometimes following normal leaves; fertile bracts similar to leaves, spreading, 2–3 mm long; the shiny brown *seeds c.* 4 mm long, fully exposed, often in pairs.

Distr. Solomon Islands (Bougainville); in *Malesia*: New Guinea (incl. New Britain), Central E.

Fig. 18. *Dacrydium xanthandrum* PILGER. a. Female shoot with seed-bearing structure, ×1.5; b. portion of twig, ×6; c. seed-bearing structures and seed, ×1.5 (after KOCHUMMEN FRI 29472).

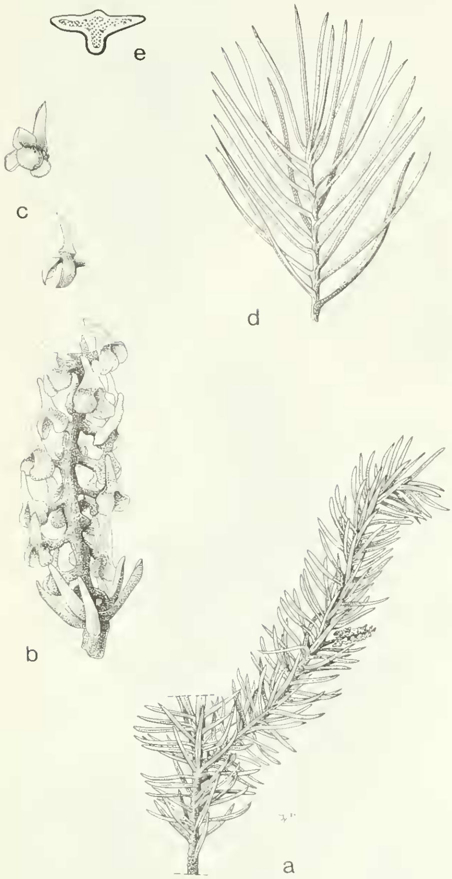

Fig. 19. *Dacrydium xanthandrum* PILGER. a. Male shoot with pollen cone, ×0.5; b. pollen cone, ×6; c. microsporophylls, ×1.5; d. juvenile shoot with leaves, ×1.5; e. leaf in cross section, ×15 (*a–c* S 37067; *d–e* DE LAUBENFELS P627).

Celebes (2 coll.), Philippines (Mindoro, 1 coll.), Borneo (Sabah; Central Kalimantan: Bt. Raya; Sarawak: Mt Mulu, Mt Murud), N. Sumatra (Atjeh, 1 coll.), and Malaya. Locally discontinuous. Fig. 20.

Ecol. Locally common or even dominant and shrubby on mossy ridges with peaty soils over clay, sand, granite, sandstone, or dacite, or scattered larger individuals in nearby primary forest from (500–) 1000–2700 m.

Vern. Sabah: *kerapui*, Dusun, Sensuron, *seringoun*, Bokan, Mt Alab, *arun gunong*, Atjeh.

Note. See comments under *D. beccarii*. The distinctly bifacially flattened leaves, generally concave

Fig. 20. Range of *Dacrydium xanthandrum* PILGER.

on the axial surface, contrast strongly with the fine and distinctly more crowded leaves of *D. beccarii*. The difference is particularly noticeable on young plants. Fertile structures, like new shoots, are normally produced as is usual in the family after a period of rest but the examples of terminal seed-bearing structures without the usual subtending short shoot with reduced leaves apparently have appeared without the intervening rest period.

13. Dacrydium comosum CORNER, Gard. Bull. S. S. 10 (1939) 244, t. 10; Wayside Trees (1940) 721; DE LAUB. J. Arn. Arb. 50 (1969) 307; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1b; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 36 , f. 684.

Shrub *c.* 2–4 m tall, 5 cm diam., on exposed ridge, to a tree at least 12 m tall. Densely branched with branches all turning upward and the aggregated tufts forming a nearly flat to umbrella-like crown. *Juvenile leaves* spreading perpendicular to the branch and then curving forward ± parallel with the branch, pungent, lanceolate, up to 33 mm long and *c.* 0.8 mm wide at the base, 0.2 mm thick, sharply keeled on the dorsal side, nearly flat or slightly concave on the axial side. *Adult leaves* similar to juvenile leaves except that the upper part is usually straight so that the apices are directed somewhat outward, 12–20 mm long, 0.6–1 mm wide but slightly expanded at the basal attachment, 0.2 mm thick. *Fertile structures* mostly lateral, subtended by a small cluster of reduced leaves which are *c.* 4 mm long. *Pollen cones* 8–10 mm long and *c.* 3 mm diam.; apex of the microsporophyll a narrow lanceolate spur 1.5–2 mm long and *c.* 0.5 mm wide. *Seed-bearing structure* consisting of several lanceolate bracts *c.* 2 mm long, one or two of which are usually fertile. The light brown, fully exposed *seeds* are 4–5 mm long.

Distr. *Malesia*: Malaya (known only from the crest separating Selangor and Pahang and on the G. Tahan massif; Pine Tree Hill; Ulu Kali; Ginting Highland). Fig. 21.

Ecol. On exposed ridges as a local dominant in stunted mossy forest between 1440 and 2200 m.

Fig. 21. Range of *Dacrydium comosum* CORNER (dots) and *D. ericoides* DE LAUB. (triangles).

14. Dacrydium ericoides DE LAUB., *nov. sp.*

Arbor ad 17 m alta. Folia linearia recta, paginis superis planis, apicis abruptis apiculatis, 5–10 mm longa, 0.7–1 mm lata, 0.2 mm crassa, dorsis carinatis. Strobili fere laterali, masculi 7–10 mm longi, 2–2.5 mm diametri, apicis microsporophyllorum calcaria 1 mm longa. Type: BRUNIG S 8722 (L, holo), Merurong Plateau, Sarawak.

Tree 10–17 m tall, 25–30 cm diam., with drooping twigs. *Leaves* linear, straight, spread out more or less perpendicular to the shoot except on new growth, narrowing abruptly at the apex to an apiculate tip, flat on the upper surface but becoming slightly concave towards the apex, stomata on the upper surface in two bands separated over the midvein, sharply keeled on the lower surface, 5–10 mm long, 0.7–1 mm wide, 0.2 mm thick. *Fertile structures* usually lateral, subtended by a cluster of reduced leaves which are 2–3 mm long. *Pollen cones* 7–10 mm long and 2–2.5 mm diam. Apex of the microsporophyll a lanceolate spur *c.* 1 mm long and 0.7 mm wide. Seed bracts 3–4 mm long with sometimes two fertile. Mature *seed* unknown.

Distr. *Malesia*: Borneo (Sarawak, known only from Mt Dulit and the Merurong Plateau in N. Sarawak). Fig. 21.

Ecol. Locally common in primary forest on exposed mossy ridges at 1000 to 1500 m.

Vern. *Sempilor*, Bintulu.

Note. The spreading straight linear leaves contrast rather strikingly with other members of the genus and rather resemble the juvenile foliage of *Cupressaceae*. Earlier I had included it in *D. spathoides* where the shorter leaves are also more or less linear and much wider than thick, but in this species the fertile structures are usually terminal and are subtended by nearly typical leaves not greatly reduced as in *D. ericoides*, while the leaves are distinctly bent forward and not straight.

15. Dacrydium leptophyllum (WASSCHER) DE LAUB., *nov. comb.* — *Podocarpus leptophylla* WASSCHER, Blumea 4 (1941) 414, t. 4, f. 9. — *Dacrycarpus leptophylla* (WASSCHER) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 150.

Leaves diverging widely from the stem but sharply bent forward parallel to the stem or even directed inward, lanceolate, pungent, 1–1.5 mm long, 0.2–0.3 mm wide, 0.1 mm thick, strongly keeled on the dorsal side, flat or slightly concave on the axial side. Leaves on vigorous branches larger, up to 3 mm long and 0.6 mm wide. Fertile material unknown.

Distr. *Malesia*: West New Guinea (known only from the top of Mt Goliath), at 3000–3600 m.

Note. The original description expressed uncertainty between *Dacrydium* and *Podocarpus sect. Dacrycarpus* for this unique taxon, but unfortunately settled for the latter. The tiny leaves are typical for *Dacrydium* and the primary branches show no sign of the dimorphism which characterizes *Dacrycarpus*.

3. FALCATIFOLIUM

DE LAUB. J. Arn. Arb. 50 (1969) 308; Fl. Nouv. Caléd. et Dép. 4 (1972) 30; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 67. — **Fig. 22.**

Dioecious shrubs to large trees to 36 m tall with thin more or less smooth brownish bark with scattered lenticels, reddish and somewhat fibrous within, breaking off in occasional flakes on larger specimens. Loosely and irregularly branched. *Leaves* spirally placed, single veined, and alternating with elongated appressed scales which are loosely clustered at the shoot apices to form foliar buds between episodes of growth. *Seedling leaves* narrowly lenticular, apiculate, bifacially flattened, giving way abruptly to distinct juvenile leaves in about the second year of growth. *Juvenile and adult leaves* distichous, bilaterally flattened and falcately curved away from the branch with the apex in most cases oppositely curved in the direction of shoot growth. *Reproductive struc-*

tures on short scaly shoots which are either axillary or terminal and may bear a few reduced leaves. *Pollen cones* cylindrical, solitary or clustered; microsporophyll a small acuminate spur above the two pollen sacs. *Seed-bearing structures* solitary, consisting of up to about a dozen large acuminate scales which become greatly swollen, red, and fleshy when mature; normally one subapical scale fertile with a cup-shaped epimatium which has a distinct hump opposite the base of the included *seed* positioned well beyond the subtending fleshy scale so that the solitary seed and its basal humped epimatium are fully exposed; the inverted ovule gradually turning upward as it matures into a nearly erect seed; the *mature seed* with two lateral weak ridges along its wider sides which come together in an apical ridge, otherwise the seed is more or less egg-shaped.

Distr. New Caledonia (1 *sp.*); in *Malesia*: New Guinea, Moluccas (Obi I.), N. & Central Celebes, Philippines (Mindoro), Borneo, Riouw-Lingga Arch. (Lingga), and Malaya.

Note. Obviously related to *Dacrydium* but differing in the dimorphic foliage with specialized fertile shoots and the exposed hump of the epimatium opposite the base of the seed. In *Dacrydium* the base of the seed lies close to its attachment and is always well covered by the subtending bract.

KEY TO THE SPECIES

1. Adult leaves normally bent at least slightly forward at the apex, tapering from at least the centre of the leaf; pollen cones at least 17 mm long.
2. Adult leaves linear-lanceolate, sun leaves at least 20 mm long, not glaucous; pollen cone 2.5–3.5 mm diam. . . . . **1. F. falciforme**
2. Adult leaves mostly lanceolate, sun leaves 13–20 mm long, glaucous; pollen cone 1.5–3 mm diam. **2. F. gruezoi**
1. Adult leaves often not bent forward at the apex, the sides parallel for most of their length; pollen cones no more than 13 mm long.
3. Adult leaves weakly keeled if at all, 2–3.5 mm wide, 12–20 mm long . . . . **3. F. papuanum**
3. Adult leaves distinctly keeled on their broader surfaces, 1–2.5 mm wide, 18–35 mm long **4. F. angustum**

1. Falcatifolium falciforme (PARL.) DE LAUB. J. Arn. Arb. 50 (1969) 309; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 73. — *Podocarpus falciformis* PARL. in DC. Prod. 16, 2 (1868) 685. — *Nageia falciformis* (PARL.) O.K. Rev. Gen. Pl. 2 (1891) 800. — *Dacrydium falciforme* (PARL.) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 45; FOXW. Philip. J. Sc. 6 (1911) Bot. 153; RIDLEY, J. Str. Br. R. As. Soc. *n.* 60 (1911) 56; PILGER, Bot. Jahrb. 54 (1916) 35; STAPF, J. Linn. Soc. Bot. 42 (1914) 191, f. 8; BURKILL & HOLTTUM, Gard. Bull. S. S. 3 (1923) 76; RIDLEY, Fl. Mal. Pen. 5 (1925) 280; CORNER, Wayside Trees (1940) 722; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 2. — **Fig. 22.**

Large shrub from 1.5 m to occasionally a large tree as much as 36 m tall, more commonly 5–12 m, 4–40 cm diam. *Seedling leaves* widening gradually from a petiole several mm long to margins parallel in the middle of the leaf, apex more abrupt, acute, apiculate, midrib a low blunt ridge above and a narrow sharp ridge below, slightly revolute, 4–9 by 2–3.5 mm. *Juvenile leaves* on the first branches only slightly longer and wider than the seedling but soon becoming as much as 12 cm long and more gradually becoming as much as 12 mm wide, the lanceolate apex strongly curved so as to become parallel to the shoot, midribs on either side a weak ridge. *Adult shade leaves* spreading at a large angle with more or less parallel margins in the centre of the leaves and broadly lanceolate apex which curves strongly forward but still at an angle from the shoot, 4–7 cm by 5–9 mm. *Adult sun leaves* much more abrupt at both ends so as to form a broad lens shape to almost a parallelogram with rounded corners, 2–4 cm long by 5–7 mm wide, the apex sometimes not bent forward. *Pollen cones* 2–4 cm long by 2.5–3.5 mm diam. Receptacle of *seed-bearing structure* 4–5 mm long; mature *seed* 6–7 mm long, 5 mm wide, and 3.5–4 mm thick, becoming black.

Distr. *Malesia*: Malaya, Riouw-Lingga Arch. (Lingga: P. Tanda) and Borneo (mainly Sarawak and Sabah). Fig. 23.

Ecol. Locally common along ridges as a bushy tree or in the subcanopy of primary rain-forest, often

Fig. 22. *Falcatifolium falciforme* (PARL.) DE LAUB. Twig with male cone, × 1 (after WYATT-SMITH KEP 93115).

on podsol sands and kerangas, but occasionally on deeper fertile soils a somewhat emergent forest giant, from 400–2100 m.

Vern. *Kayu china*, Sabah, Lahad Datu, *iguh gawah*, Iban, Merurong Plateau.

Notes. In the forests of Mt Kinabalu the juvenile plants have smaller leaves than elsewhere, but otherwise there do not appear to be any differences. Several collections of more or less juvenile material have been made in Celebes and Central Moluccas (Obi), but these resemble more *F. gruezoi* of the Philippines. A single specimen from high kerangas on the Usan Apan Plateau in Sarawak has leaves in the form of adult shade leaves, but these are only 6 by 2 mm. It is called a 'young tree' but given as 24 m tall. This may well be a new species.

2. Falcatifolium gruezoi DE LAUB., *nov. sp.* — *Dacrydium falciforme* [*non* (PARL.) PILGER] FOXW. *ex* MERR. Philip J. Sc. 2 (1907) Bot. 257; FOXW. *ibid.* 6 (1911) Bot. 153, t. 28, f. 1; MERR. En. Philip. 1 (1922) 4.

Arbor 4–12 m alta. Folia juvenilia ad 7.5 cm longa, 7 mm lata, falcata et apice versus apex ramorum curvo, lanceolata; folia adulta umbrae minora, 3.5 cm longa, 6–7 mm lata; folia solis plus minora, 13–20 mm longa, 3.5–6 mm lata, acuta, apiculata, glauca. Strobili masculi 1.7–6 cm longi, 1.5–3 mm diametri. Strobili feminei receptaculo 2 mm, semina 7 mm longo. Type: GRUEZO WM 4052 (L, holo; CALP, iso), Naujan, Paitan access, Paitaraan (Mt Halcon area), Mindoro Oriental, Philippines.

Tree 4–12 m tall. *Juvenile leaves* to 7.5 cm by 7 mm, falcate with the apex curved forward more or less parallel with the branch; lanceolate. *Adult leaves* in the shade smaller, 3.5 cm by 6–7 mm; sun leaves even smaller, 13–20 by 3.5–6 mm, acute, apiculate, glaucous. *Pollen cones* 1.7–6 cm long and 1.5–3 mm diam. *Receptacle* of the *seed-bearing structure* 2 mm long; seed 7 mm long.

Distr. *Malesia*: Philippines (Luzon: Tayabas, Nueva Ecija; Mindoro; Panay; Mindanao: Davao, Surigao); Celebes: Manado (Poso; Gorontalo; Palu); Moluccas (Obi). Fig. 23.

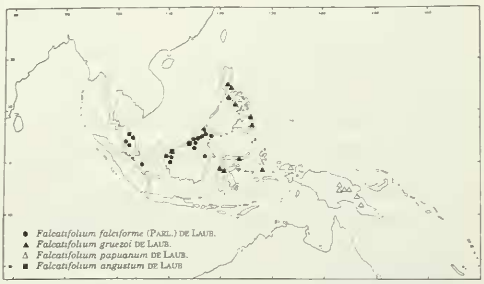

Fig. 23. Range of four spec~~ies of the genus~~ *Falcatifolium*.

Ecol. In exposed locations along ridges or on the borders of open areas, 1600–2200 m in the Philippines, 1200–1400 m in Celebes, 700 m in Obi.

Note. See note under *F. falciforme*.

3. Falcatifolium papuanum DE LAUB. J. Arn. Arb. 50 (1969) 312, f. 6; Blumea 17 (1969) 274; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 73, f. 698. — *Dacrydium falciforme* [*non* (PARL.) PILGER] LAUT. Bot. Jahrb. 68 (1937) 247.

Tree 6–22 m tall, 8–40 cm diam. *Seedling leaves* 6–18 by 0.6–0.8 mm. *Juvenile leaves* the same as the smaller adult leaves, glaucous beneath. *Adult leaves* falcate and then more or less linear in the distal part of the leaf or tapering slightly, narrowing almost abruptly to an apiculate apex, the apex occasionally bent slightly forward, 10–20 by 2–4 mm. *Pollen cones* 5–13 mm long and 2–2.5 mm diam. *Receptacle* and *seed* each 6–7 mm long.

Distr. *Malesia*: New Guinea. Fig. 23.

Ecol. Understory tree of moist mountain forests, often associated with *Nothofagus spp.*, *Myrtaceae* and other *Podocarpaceae*, 1500–2400 m.

Vern. *Mungag*, Hagen Togoba, *tugl*, Wahgi, Minj.

Note. An entire plant scarcely 20 cm tall with tiny leaves mentioned and illustrated in the type description from the Vogelkop either represents perhaps a reduced form of exposed ridges or a distinct new species.

4. Falcatifolium angustum DE LAUB. J. Arn. Arb. 50 (1969) 312, f. 7a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 73, f. 699.

Tree to 20 m tall, 6–25 cm diam. *Juvenile leaves* narrowly lanceolate and gradually curved slightly forward towards the apex, *c.* 7 cm long and 1.2 mm near the base. *Adult leaves* less curved or straight, pungent, keeled on each side, 18–35 by 1–2.5 mm. Somewhat immature *pollen cones* 8 mm long and 2 mm diam. Seed-bearing structures unknown.

Distr. *Malesia*: Borneo (known from two locations near the coast of Sarawak). Fig. 23.

Ecol. In forests, 90–240 m, on podsolized sands and kerangas, associated with *Parastemon*, *Shorea albida*, and *Gymnostoma sp.*

4. DACRYCARPUS

(ENDL.) DE LAUB. J. Arn. Arb. 50 (1969) 315; Fl. Nouv. Caléd. et Dép. 4 (1972) 34; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 133; DE LAUB. Kalikasan 7 (1978) 125; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 11. — *Podocarpus sect. Dacrycarpus* ENDL. Syn. Conif. (1847) 221; CARRIÈRE, Traité Gen. Conif. ed. 1 (1855) 477; ed. 2 (1867) 676; GORDON, Pinetum ed. 1 (1858) 289; ed. 2 (1875) 356; MIQ. Fl. Ind. Bat. 2 (1859) 1074; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 403; DE BOER, Conif. Arch. Ind. (1866) 25; PARL. in DC. Prod. 16, 2 (1868) 520; DE KIRWAN, Conif. 2 (1868) 224; EICHLER in E. & P. Nat. Pfl. Fam. II, 1 (1889) 105; BEISSNER, Nadelholzkunde (1891) 17; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 55; in E. & P. Nat. Pfl. Fam., Nachtr. 3 (1908) 3; FOXW. Philip J. Sc. 6 (1911) Bot. 156; STILES, Ann. Bot. 26 (1912) 448; GIBBS, Ann. Bot. 26 (1912) 525; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 242; HICKEL, Fl. Gén. I.-C. 5 (1931) 1066; WASSCHER, Blumea 4 (1941) 386; BUCHHOLZ & GRAY, J. Arn. Arb. 29 (1948) 56. — *Podocarpus sect. Dacrydioideae* BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 41. — *Podocarpus sect. Dacrydium* BERTRAND, Ann. Sc. Nat. V, 20 (1874) 67. — **Fig. 26, 28, 31–33.**

Dioecious shrubs or trees, to 41 m tall. Bark hard, dark brown or blackish but weathering to gray, surface rough with occasional lenticels, inside pink to reddish brown and granular or slightly fibrous, on older trees breaking off in small thick, somewhat vertically elongated plates or sometimes short strips. *Leaves* amphistomatic, spirally placed, broadly decurrent, apiculate. Leaves on primary shoots as well as on the basis of foliage shoots and fertile structures bifacially flattened, keeled on the dorsal side, lanceolate or sometimes triangular, often nearly appressed, mostly 1.5–3 by 0.5–0.8 mm, but wider on the decurrent part, up to at least 4 mm long on young plants and mostly 1–2 mm long at the base of foliage shoots or fertile structures. The apex of resting shoots a loose cluster of reduced leaves. *Juvenile type of leaves* on special shoots that generally do not continue growth after reaching a resting stage, bilaterally flattened and usually slightly keeled on both faces, falcate and then curved forward towards the apex so that the apiculate tip is oriented more or less parallel with the shoot, otherwise linear or less often lanceolate, spreading at about a 60° angle, the centre of the leaf either straight or gradually curving to the tip, distinctly shorter towards either end of the shoot so that the whole shoot has a feather-like appearance, mostly 6–12 mm long and *c.* 1 mm wide, usually distichous, gradually changing to an adult form but often fertile at intermediate stages of this transition. *Final adult forms* not distichous, generally shorter and more robust than the juvenile leaves, more or less uniform along the shoot, the apiculate tip still bent forward parallel to the shoot, in some species nearly identical with the leaves of primary shoots. *Fertile structures* terminal on short, mostly lateral shoots, the seed-bearing structures usually on a considerably longer shoot than that of the pollen cone. Immature *pollen cones* at first sometimes nearly spherical, then becoming somewhat elongated but finally elongating abruptly with a slight decrease in diameter at maturity, then mostly *c.* 6–10 mm long and 2–3 mm diam., sometimes longer. Apex of microsporophyll triangular, acute to apiculate, *c.* 1.2 by 0.8 mm. *Shoots for female structures* 3–17 mm long. Leaves at the base of the seed-bearing structure sharply elongated to form an involucre which often surrounds the immature seed-bearing structure but which in the shorter examples becomes spreading as the structure grows. *Seed-bearing structure* composed of a small warty receptacle, 2.5–4 mm long, 2.5 mm diam., which becomes greatly enlarged, fleshy, and first orange then red or in other species purple when ripe, later turning brown, bearing one or two protruding short sterile leaf-like bracts and one or two subterminal fertile bracts. The *inverted ovules* completely surrounded by the epimatium and fused as a rib along one side with the fertile bract whose short free tip forms a small off-centre crest over the mature structure. *Mature seed* nearly spherical (or oval) but remaining covered by the leathery epimatium and scale, forming an erect or somewhat oblique structure which in most species is *c.* 5–6 mm long and 4.5–5.5 mm diam., dark in colour.

Distr. Ranging from northern Burma and southernmost China to Fiji and New Zealand 9 *spp.*; in *Malesia* abundant with 7 *spp.*, reaching their greatest variety in New Guinea with 5 *spp.* Fig. 24.

Fossils are known from N. Antarctica (Graham Land) and New Zealand (Middle Jurassic) and S. Patagonia (Upper Cretaceous to Oligocene) where the genus is now extinct. In the Eocene found in New Zealand, and since the Oligocene also in SE. Australia, where it became extinct (FLORIN, Kongl. Svensk. Vet. Ak. Handl. III, 19, *n.* 2, 1940, 70; Acta Horti Berg. 20 (4), 1963, 188, f. 19: map).

Note. Sterile specimens strongly resemble *Dacrydium* and hence the generic name. The fusion of the fertile scale with the epimatium is a unique trait of the genus while the seeds of *Dacrydium* are furthermore naked. In most cases sterile specimens can be readily distinguished from *Dacrydium* by the distinctly dimorphic foliage.

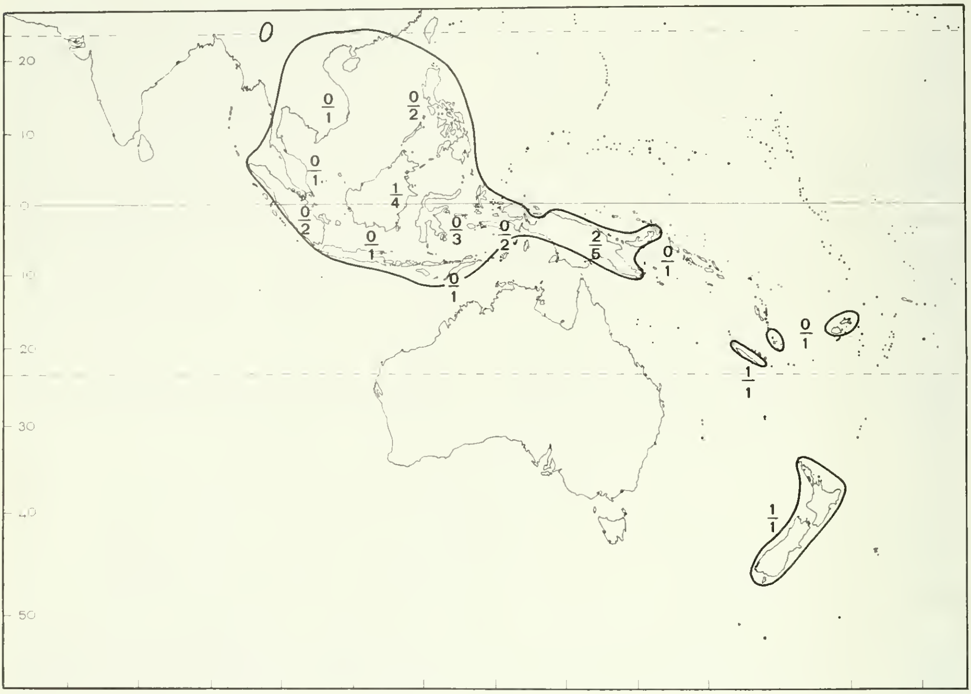

Fig. 24. Range of the genus *Dacrycarpus* (ENDL.) DE LAUB. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

KEY TO THE SPECIES

1. Involucral leaves short (2.5–5 mm long) and mostly spreading so that the immature receptacle becomes or more frequently is always exposed; adult leaves scale-like or equally keeled on four sides, 1–3 mm long.
  2. Adult leaves less than 2 mm long, more or less in the form of scales .... **1. D. imbricatus**
  2. Adult leaves at least 2 mm long, in the form of short needles .... **2. D. steupii**
1. Involucral leaves curved to surround the young fertile structure (3–13 mm long) and still covering at least the entire immature receptacle before it enlarges when ripe; adult leaves not scale-like nor equally keeled on four sides, 1–6 mm long.
  3. Adult leaves bilaterally flattened.
    4. Involucral leaves surrounding receptacle and mature seed (7–13 mm long); foliage leaves slender (0.6–0.8 mm wide), scarcely keeled .... **3. D. cumingii**
    4. Involucral leaves reaching the base only of the mature seed (5–8 mm long); foliage leaves robust (0.8–1 mm wide), strongly keeled .... **4. D. kinabaluensis**
  3. Adult leaves bifacially flattened.
    5. Involucral leaves less than 5 mm long, not reaching the mature seed; foliage leaves 0.6–1 mm wide.
      6. Seed not large (5–6 mm long); foliage leaves spreading .... **5. D. expansus**
      6. Seed large (7–8 mm long); foliage leaves imbricate .... **6. D. compactus**
    5. Involucral leaves 6–10 mm long, mostly covering the mature seed; foliage leaves 0.4–0.6 mm wide **7. D. cinctus**

1. Dacrycarpus imbricatus (BLUME) DE LAUB. J. Arn. Arb. 50 (1969) 320, f. 8a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 152, f. 724; DE LAUB. Kalikasan 7 (1978) 126; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 13. — *Podocarpus imbricatus* BLUME, En. Pl. Jav. 1 (1827) 89; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 56; KOORD. Exk. Fl. Java 1 (1911) 64, f. 2; Atlas 3 (1915) f. 585, 586; Fl. Tjibodas (1918) 3; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245, f. 124E; HICKEL, Fl. Gén. I.-C. 5 (1931) 1068; STEEN. Trop. Natuur 29 (1940) 75, 1 fig.; WASSCHER, Blumea 4 (1941) 388, t. 111, f. 2; BACKER & BAKH.*f.* Fl. Java 1 (1963) 89; STEEN. Mount. Fl. Java (1972) t. 13, f. 2. — *Podocarpus cupressina* R.BR. *ex* MIRBEL, Mém. Mus. Hist. Nat. Paris 13 (1925) 75, *nomen*; BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 35, f. 10; ENDL. Syn. Conif. (1847) 222; BLUME, Rumphia 3 (1847) 218, t. 172, f. 2 & t. 172B, f. 2; MIQ. Pl. Jungh. 1 (1851) 3; Fl. Ind. Bat. 2 (1859) 1074; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 403; DE BOER, Conif. Arch. Ind. (1866) 25; PARL. in DC. Prod. 16, 2 (1868) 521; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 106; HOOK.*f.* Fl. Br. Ind. 5 (1896) 650; WARB. Monsunia 1 (1900) 191; K. & V. Bijdr. Booms. Java 10 (1904) 262. — *Podocarpus javanicus* (*non* BURM.*f.*) MERR. Philip J. Sc. 19 (1921) 338; En. Philip. 1 (1922) 3. — **Fig. 26.**

KEY TO THE VARIETIES

1. Leaves slender (0.4–0.6 mm wide); involucral leaves always spreading.
 2. Leaves imbricate .... **a.** *var.* **imbricatus**
 2. Leaves spreading .... **b.** *var.* **patulus**
1. Leaves robust (0.6–1 mm wide); involucral leaves sometimes clasping the receptacle.
 3. Leaves spreading .... **c.** *var.* **robustus**
 3. Leaves imbricate............ **d.** *var.* **curvulus**

a. *var.* **imbricatus**

Majestic columnar tree to 50 m tall, up to 2 m diam., crown large, often dome-shaped. Leaves of primary shoots imbricate; leaves of juvenile foliage shoots distichous, nearly linear, up to 10–17 mm long by 1.2–2.2 mm wide at the centre of a shoot, gradually losing the distichous habit as the tree matures, but shoots with more or less bilaterally flattened leaves distinctly longer in the middle of the shoot almost always present on even the oldest trees. Terminal shoots on young plants often elongated whip-like up to 20 cm. Leaves on older trees eventually becoming mostly scale-like, imbricate, distinctly keeled on the dorsal side, long-triangular, 1–1.8 by 0.4–0.6 mm. Involucral leaves becoming spreading, acicular, 2.5–4 mm long, rarely to 5 mm. Ripe receptacle red.

Distr. *Malesia*: Java, all Lesser Sunda Islands (Bali–Timor) and SW. & Central Celebes. Fig. 25.

Ecol. Mostly scattered and common in primary and secondary rain-forest, not rarely as an emergent, and co-dominant in West Java with *Podocarpus neriifolius* and *Altingia noronhae*, on the south slope of Mt Tjeremai volcano characterizing the zone between 2400–2700 m without other co-dominants, a situation not yet explained (VAN STEENIS, 1972), in Timor found under more or less seasonal conditions in isolated specimens laden with *Usnea* in grassland after deforestation, mostly between 1000–2500 m,

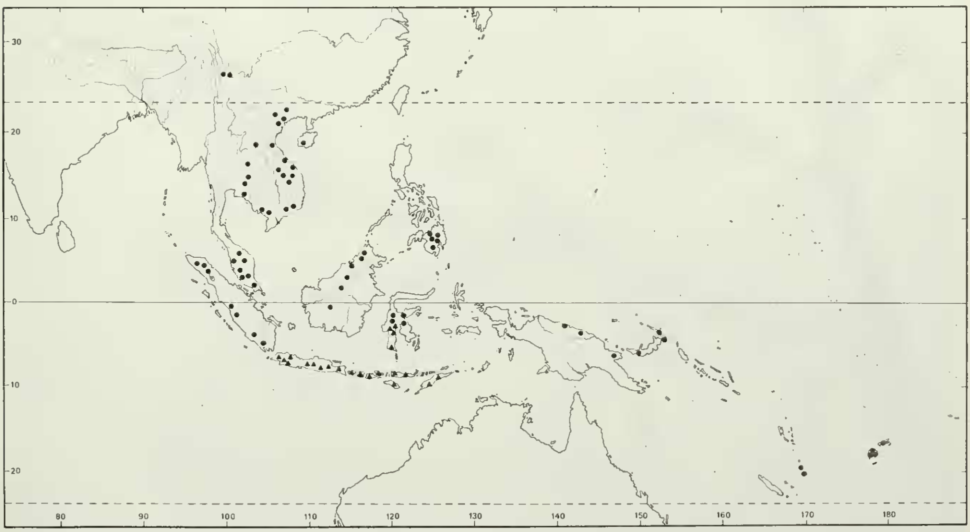

Fig. 25. Range of *Dacrycarpus imbricatus* (BLUME) DE LAUB. *var. imbricatus* (triangles) and *var. patulus* DE LAUB. (dots).

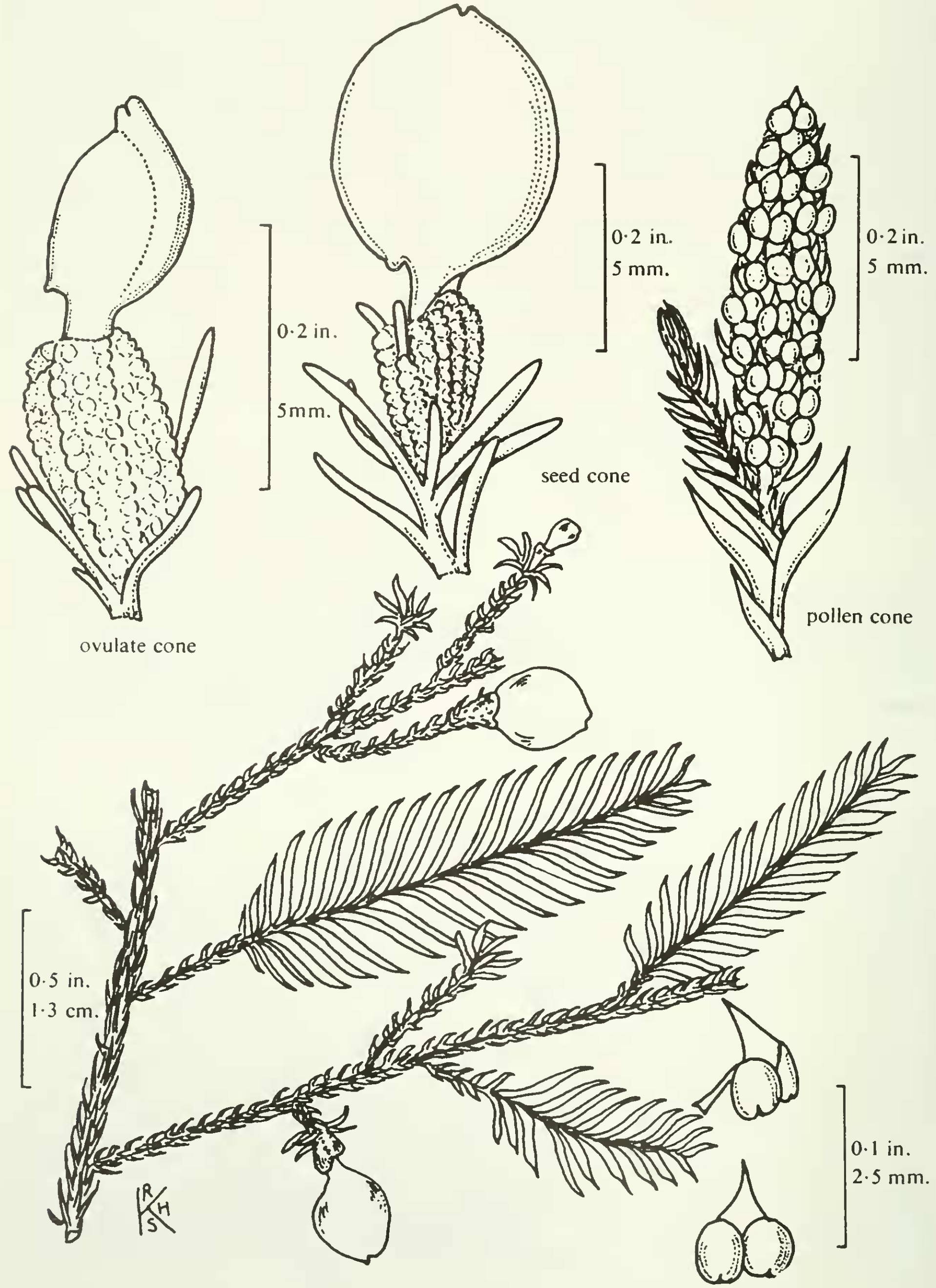

Fig. 26. *Dacrycarpus imbricatus* (BLUME) DE LAUB. *var. patulus* DE LAUB. (drawing by R.S.KENG in Whitmore, Tree Flora of Malaya 1, 1972, 51, f. 4).

but in Lombok reported as low as 200 m and in Celebes ascending to 3000 m. Probably exterminated at lower elevations in Java by deforestation. Male flowers at Tjibodas in Aug.–Sept. Sometimes the stem of full-grown trees produces sprouts at the base (VAN STEENIS, 1940).

Uses. A most valuable timber tree.

Vern. Java: *djamudju, ki hadji, ki putri, tjemoro (tukung)*, Tjidadap, S; *kadju pakis, tjemara binèh*, Md.; SW. Celebes (Bonthain): *kayu angin, k. parang*; Lesser Sunda Islands: Bali: *tarupanda*; Sumba: *kayu awama*, Lairondja, *kadju uamang*; Lombok: *majangmekar*; Flores: *oh-ru*, Ruteng; Timor: *haae tuni*, W. Timor, Nenas, *ai-caqueu fuie*, E. Timor, Tetun lang.

b. *var.* **patulus** DE LAUB. J. Arn. Arb. 50 (1969) 320, f. 8b. — *Podocarpus cupressina* RIDLEY, J. Str. Br. R. As. Soc. *n.* 60 (1911) 58. — *Podocarpus imbricatus sensu* GIBBS, Ann. Bot. 26 (1912) 525, t. 49, f. 1–8; STAPF, J. Linn. Soc. Bot. 42 (1914) 193; MERR. En. Born. Pl. (1921) 31; RIDLEY, Fl. Mal. Pen. 5 (1925) 283; MERR. Contr. Arn. Arb. 8 (1934) 14; CORNER, Wayside Trees (1940) 723; KENG in Whitmore, Tree Fl. Malaya 1 (1972) 51, f. 4. — *Podocarpus kawaii* HAYATA, Bull. Econ. Indochine 20 (1917) 439. — *D. kawaii* (HAYATA) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 140, f. 726. — **Fig. 26.**

Tree, 5–40 m tall, 10–100 cm diam. Adult foliage leaves not imbricate, spreading sharply, acicular, distinctly keeled on four sides, 0.8–1.5 by 0.4–0.6 mm. Involucral leaves to 3 mm long, spreading.

Distr. Northern Burma and southernmost China, through Southeast Asia to *Malesia*: Sumatra, Malaya, Borneo, Philippines (Luzon, Mindanao), Central Celebes, along the N. coast of New Guinea (incl. New Britain and New Ireland), and New Hebrides to Fiji. Common, but not in Java. Fig. 25.

Ecol. Scattered and common in primary and secondary rain-forest, mostly between 700 and 2500 m, in N. Sumatra at *c.* 400 m on sinterlimestone near sulphur springs near Tinggi Radja, up to *c.* 3000 m in Borneo, and occasionally to near sea-level in Fiji.

Vern. Malaya: *ru bukit*, Kedah; Sumatra: *ambun*, Solok, W. Coast, *balanidju*, Kerintji, *beru*, Karo Lands, *ki mèrak, marak*, Bencoolen, *damanik*, Simelungun, *sampinur bunga*, Karo-Toba, *talas*, Kroë, Bencoolen; Borneo: *menjilu*, Dusun lang., Kp. Tindai, Sabah, *tampilas*, Sensurun, Sabah, Dusun lang.; Celebes: *siozi*, Mt Wuka Tampai, Palu.

Note. Only in Celebes is there an overlap with *var. imbricatus* with possibly transitional forms. In Borneo, Mindanao, and along the northern coast of New Guinea specimens approach *var. robustus* in form. Specimens from the western and eastern parts of the range are identical and easily distinguishable from other varieties.

c. *var.* **robustus** DE LAUB. J. Arn. Arb. 50 (1969) 323, f. 8c; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 16, f. 35d–g. — *Podocarpus imbricatus sensu* FOXW. Philip J. Sc. 6 (1911) Bot. 157. — *Podocarpus papuanus* RIDLEY, Trans. Linn. Soc. London 11, 9 (1916) 158; GIBBS, Contr. Phytogeogr. Arfak Mts (1917) 80, f. 4; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245; Bot. Jahrb. 68 (1937) 244; WASSCHER, Blumea 4 (1941) 402, t. 4, f. 3. — *Podocarpus javanica sensu* MERR. Philip J. Sc. 19 (1921) 338; En. Philip. 1 (1922) 3, *pro specimina.* — *Podocarpus cupressina sensu* LANE-POOLE, For. Res. Terr. Papua & New Guinea (1925) 73. — *D. papuana* (RIDLEY) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 142, f. 731. — *D. steupii* (*non* DE LAUB.) DE LAUB. Kalikasan 7 (1978) 127.

Tree, 5–45 m tall, 5–130 cm diam. Adult foliage leaves like *var. patulus* but distinctly more robust, 1.2–1.8 by 0.6–0.8 mm. Involucral leaves to 3 mm long and spreading or in some areas to 5 mm and more or less clasping the receptacle.

Distr. *Malesia*: Borneo (Sarawak, once), Philippines (Luzon, Mindanao), Moluccas (Morotai, Ceram), and throughout New Guinea. Fig. 27.

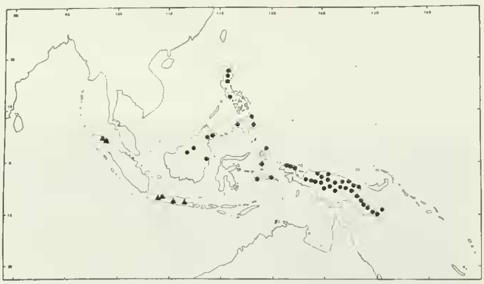

Fig. 27. Range of *Dacrycarpus imbricatus* (BLUME) DE LAUB. *var. robustus* DE LAUB. (dots) and *var. curvulus* (MIQ.) DE LAUB. (triangles).

Ecol. Scattered and, in New Guinea, very common in primary and secondary rain-forest, canopy tree, or sometimes emergent, often co-dominant, in mossy forest associated with *Nothofagus* and *Phyllocladus*, also in *Lithocarpus-Castanopsis* mixed forest co-dominant, (500–)700–3000 m, a specimen from Borneo reported from 240 m.

Vern. Borneo: *pierur*, Sarawak, Kelabit lang.; Philippines: *tupi*, Cotabato, Mindanao; West New Guinea: *apé*, Wissel Lakes, Kapauko lang., *betjhiea*, Arfak, Hattam lang., *jamari*, Wondiwoi Mts, Wandammen lang., *kaowie, kowi(e)*, Ransiki, Manikiong lang., *nijoop*, Kebar lang., *toromoai*, Dojodial, Cycloop Mts; East New Guinea: *gubin, kubin*, Hagen Togoba, *iljo*, Enga lang., *kaibelpiti*, Waghi, Minj, *lou*, Wabag lang., *pau*, Lake Inim, Enga lang., *tibuidi*, Anga Valley, Mendi lang., *uba*, Chimbu, Masul, *umba*, Waimambuno, *paupeepeen*, Mt Ne.

Note. Specimens from Borneo and the Philippines have been identified as *D. steupii* where the foliage leaves fall within the size range of this species because in these areas the distichous habit is lost rather early causing the foliage to resemble *D. steupii* closely. Unlike *D. steupii*, however, the leaves range to the smaller sizes of *D. imbricatus*. The involucral leaves in these areas, unlike elsewhere in *D. imbricatus*, are at least 5 mm long and curved upward. Perhaps this material represents a distinct variety.

d. *var.* **curvulus** (MIQ.) DE LAUB. J. Arn. Arb. 50 (1969) 326, f. 8d; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 154. — *Podocarpus cupressina var. curvula* MIQ. Pl. Jungh. 1 (1851) 4; Fl. Ind. Bat. 2 (1859) 1074. — *Podocarpus imbricatus var. curvula* (MIQ.) WASSCHER, Blumea 4 (1941) 398. — **Fig. 28.**

Shrubby pyramidal tree to 8 m tall and sometimes procumbent. Foliage shoots curved downwards but main branches curved upwards. Adult foliage leaves like *var. imbricatus* but distinctly more robust, 1.2–2 by 0.8–1 mm. Involucral leaves 2.5–4.5 mm long and more or less clasping the receptacle.

Distr. *Malesia*: North Sumatra (Atjeh: Leuser complex & G. Bandahara) and western half of Java (Priangan; Diëng). Fig. 27.

Ecol. In N. Sumatra pure stands on exposed mossy mountain peaks, on blangs and steep slopes, between 2000 and 3420 m.

Vern. *Tjamarah*, J, at variance for *Casuarina* which does not occur so far west in Java.

2. Dacrycarpus steupii (WASSCHER) DE LAUB. J. Arn. Arb. 50 (1969) 328; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 158, f. 728; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 16, f. 35a–c. — *Podocarpus steupii* WASSCHER, Blumea 4 (1941) 405, t. 4, f. 4. — *Podocarpus papuanus* (*non* RIDLEY) STEUP, Trop. Natuur 27 (1938) 145.

Conical tree, 4–36 m tall, 15–100 cm diam. *Leaves* of primary shoots spreading slightly. Leaves of juvenile foliage shoots distichous, nearly linear, soon losing the distichous habit as the tree matures. Leaves on older trees eventually becoming nearly quadrangular in cross section, widely spreading, tapering slightly, uniform in size along a shoot, 2–3 by 0.4–0.6 mm. Involucral leaves becoming spreading, 3–4 mm long.

Distr. *Malesia*: Central E. Borneo (G. Beratus,

Fig. 28. *Dacrycarpus imbricatus* (BLUME) DE LAUB. *var. curvulus* (MIQ.) DE LAUB. on Mt Bandahara, Sumatra, 2500 m. Habit of branch with female cones (Photogr. W.J.J.O. DE WILDE, 1972).

near Balikpapan, once), Central Celebes (Latimodjong Mts) and throughout New Guinea. Fig. 29.

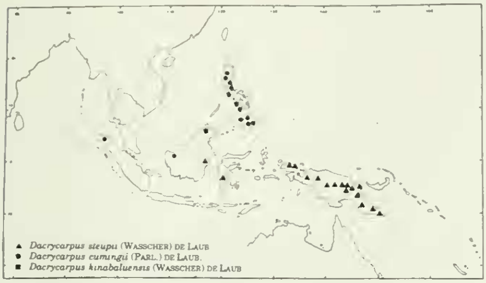

Fig. 29. Range of three species of the genus *Dacrycarpus*.

Ecol. Locally common, particularly in disturbed forests, or in poorly drained areas where it may form nearly pure stands, in boggy grasslands and reedswamps, on sandy clay, once on a rocky riverbank, once on a limestone hillock in mossy forest (Mt Beratus), 860–3420 m, but mostly *c.* 1500–2000 m.

Vern. New Guinea: *miejoop*, *nak*, Kebar lang., *apè*, Wissel Lakes, Kapauko lang., *pau*, Wabag, Enga lang.

Note. The spreading needles give this species a rather distinct appearance from *D. imbricatus var. robustus* which it otherwise strongly resembles. In New Guinea it has a markedly distinct ecology.

3. Dacrycarpus cumingii (PARL.) DE LAUB. J. Arn. Arb. 50 (1969) 329; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 156, f. 727; DE LAUB. Kalikasan 7 (1978) 128. — *Podocarpus cumingii* PARL. in DC. Prod. 16, 2 (1868) 521; WASSCHER, Blumea 4 (1941) 407, t. 4, f. 5. — *Nageia cumingii* (PARL.) O. K. Rev. Gen. Pl. 2 (1891) 800. — *Podocarpus imbricatus var. cumingii* (PARL.) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 56.

Tree, 8–25 m tall, up to 18–75 cm diam. *Leaves* of primary shoots spreading slightly, often curved so that the apex is directed inward slightly towards the axis. Leaves of juvenile foliage shoots distichous, nearly linear. Leaves of older trees similar but mostly not distichous, often more robust and scarcely keeled on the lateral faces, 3–6 by 0.6–0.8 mm. In addition to primary shoots and purely foliage shoots there are intermediate shoots with leaves 2–3 mm long, strongly keeled on four sides, but distinctly bilaterally flattened. The intermediate shoots bear foliage shoots and fertile shoots but are caducous like the foliage shoots and unlike the primary shoots. *Pollen cones* usually normal but on one specimen from low elevation up to 4 cm long. *Involucral leaves* greatly elongated resembling the foliage leaves but curved, not straight, 7–13 mm long, completely surrounding the developing fertile structure which scarcely surpasses them when fully mature. Ripe receptacle reddish.

Distr. *Malesia*: N. Sumatra (Leuser complex, 2 coll.), Borneo (Sarawak, rare), Philippines (Luzon, Negros, Panay, Mindanao). Fig. 29.

Ecol. Locally common from 1000 to 3314 m, but mostly between 1850 and 2650 m in mossy primary forest. Locally it occurs above *D. imbricatus* most of whose varieties do not enter the mossy forest.

Vern. Sumatra: *sangu*, Gajo, Mt Leuser; Philippines: *igem*, Davao, Mindanao.

4. Dacrycarpus kinabaluensis (WASSCHER) DE LAUB. J. Arn. Arb. 50 (1969) 330; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 154, f. 725. — *Podocarpus imbricatus var. kinabaluensis* WASSCHER, Blumea 4 (1941) 400, t. 4, f. 2. — *Podocarpus imbricatus* (*non* BLUME) GIBBS, Ann. Bot. 26 (1912) 525, *p.p.*, t. 49, f. 1–9.

Shrub or small, sometimes gnarled tree, 2–13 m tall, 15–30 cm diam. *Leaves* of primary shoots nearly imbricate with the apex often curved slightly inward. Leaves of juvenile foliage shoots distichous, nearly linear. Leaves on older trees similar but soon becoming not distichous and more robust, distinctly keeled on the lateral faces, 3–6 by 0.8–1 mm. Together with primary shoots and foliage shoots are intermediate shoots with leaves 2–5 mm long and triangular or quadrangular in cross section. The intermediate shoots bear foliage shoots and fertile shoots but are also deciduous. *Involucral leaves* greatly elongated resembling the foliage leaves but more distinctly curved, 5–8 mm long, reaching only the lower part of the seed when it is mature. Ripe receptacle blue or purple. *Seed* with its covering 6–7 mm long and 5–6 mm diam.

Distr. *Malesia*: Borneo (Sabah: Mt Kinabalu). Fig. 29.

Ecol. Common, sometimes in nearly pure stands in dwarf mountain scrub from 2700 m to the tree line at *c.* 4000 m.

Note. On Mt Kinabalu *D. imbricatus* does not occur above *c.* 2000 m, leaving a considerable gap before *D. kinabaluensis* is seen, which represents the mossy forest zone. In fact, *D. kinabaluensis* rather strongly resembles *D. cumingii*, differing particularly in the distinctly shorter involucral leaves. Foliage leaves of *D. cumingii* when collected from exposed parts of the tree approach this species in robust form. The receptacle colour of *D. cumingii* is poorly documented and may well become purple also.

5. Dacrycarpus expansus DE LAUB. J. Arn. Arb. 50 (1969) 334, f. 7b; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 162, f. 733.

Tree 9–25(–30) m tall, 22–58 cm diam. *Leaves* of primary shoots on young plants nearly imbricate but on older plants spreading and then curved forwards. Leaves of juvenile foliage shoots distichous, nearly linear, soon losing the distichous habit as the tree matures. Leaves on older trees eventually becoming wider than thick but distinctly keeled on the upper and lower surfaces, spreading but the upper half curving forwards, uniform in size along the shoot, tapering slightly, 1.5–3 by 0.4–0.8 mm or a little larger on younger trees. *Involucral leaves* loosely surrounding the young fertile structure but covering only the receptacle of the mature seed with its covering, which is *c.* 3–3.5 mm long.

Distr. *Malesia*: Central Highlands of Papua New Guinea. Fig. 30.

Ecol. Locally common or even in pure stands (*e.g.* at Wabag), or co-dominant, sometimes emergent, often in disturbed situations, *e.g.* on edges of treefern grassland, 1300–2750 m.

Vern. *Pa'u, pau*, Kepilan, Enga lang.

Note. Not associated with moist habitats like *D. steupii*, a species which is also associated with disturbed habitats. This latter species differs in the form of the foliage leaves and the involucral leaves.

Fig. 30. Range of *Dacrycarpus expansus* DE LAUB. (squares) and *D. compactus* (WASSCHER) DE LAUB. (dots).

6. Dacrycarpus compactus (WASSCHER) DE LAUB. J. Arn. Arb. 50 (1969) 336, f. 9c; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 158, f. 730; VAN

Fig. 31. A boggy hollow, filled with the tall grass *Deschampsia klossii* RIDLEY (*c.* 1 m high) with on the edge tall *Dacrycarpus compactus* (WASSCHER) DE LAUB. in dense, very mossy shrubberies of mixed composition. About 1 km north of Lake Habbema, West New Guinea, 3300 m (Photogr. L.J.BRASS, 1938).

ROYEN, Alpine Fl. New Guinea 2 (1979) 20, f. 36, t. 80. — *Podocarpus compacta* WASSCHER, Blumea 4 (1941) 411, t. 4, f. 8a, b. — *Podocarpus papuanus* (*non* RIDLEY) PILGER, Bot. Jahrb. 68 (1936) 244. — **Fig. 31, 32.**

Irregular tree 2–20 m tall, up to 25–60 cm diam. *Leaves* of primary shoots spreading slightly, often curved so that the apex is directed inward towards the axis. Leaves of juvenile foliage shoots not distichous, lanceolate, strongly keeled laterally, 2–2.5 by 0.6 mm. Leaves on older trees becoming similar to the leaves on primary shoots, spreading but curved through most of their length, strongly keeled on the dorsal side, 1–2.5 by 0.6–1 mm. *Pollen cones* on a 3 mm or more often longer shoot. *Involucral leaves* robust, curving to surround the receptacle, strongly keeled on the dorsal side and more or less triangular in cross section, 4–5 by 0.8–1.2 mm. *Ripe receptacle* purple to black. *Seed* with its covering 7–8.5 mm long and 7–8 mm diam.

Distr. *Malesia*: New Guinea. Common in E., but rare in W. New Guinea (Habbema Lake, Quarles Lake, 2 coll.). Fig. 30.

Fig. 32. *Dacrycarpus compactus* (WASSCHER) DE LAUB. Detail of female branch with cones. Mt Amungwiwa, New Guinea, 3050 m (Photogr. P. VAN ROYEN 11072, June 1976).

Ecol. Common on the higher peaks near the tree line, sometimes forming pure stands or emerging above a subalpine shrubbery, or scattered in alpine grassland, often in isolated specimens and obviously fire-resistant, in *Podocarpus-Libocedrus* forest, rarely on wet peaty soil (Lake Aunde), 2800–3950 m, but mostly above 3400 m.

Vern. *Kadzinam, kaibigl*, Minj, *kaipik*, Kubur, Minj, *umbwa*, Lake Aunde, Chimbu, Waimambano, *umba-nifiogo*, Chimbu, Lake Aunde.

7. Dacrycarpus cinctus (PILGER) DE LAUB. J. Arn. Arb. 50 (1969) 332, f. 9a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974), 160, f. 732; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 17, f. 35h, t. 79. — *Podocarpus cinctus* PILGER, Bot. Jahrb. 69 (1938) 253; WASSCHER, Blumea 4 (1941) 409, t. 4, f. 6. — *Podocarpus dacrydiifolia* WASSCHER, *l.c.* 410, t. 4, f. 7. — *D. dacrydiifolia* (WASSCHER) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 148, f. 729. — **Fig. 33.**

Often flat-crowned tree up to 33 m, 20–90 cm diam., or a shrub 2–4 m tall. *Leaves* of primary shoots spreading slightly, straight or more often curved forward, 5–6 mm long on young plants, becoming 3–4 mm long on adult plants and 2–3 mm long at the base of foliage shoots and fertile structures. Leaves of juvenile foliage shoots not disti-

Fig. 33. *Dacrycarpus cinctus* (PILGER) DE LAUB. Detail of female branch with cones. Papua New Guinea, Southern Highlands District, 27 miles from Mendi, 2743 m (Photogr. WOMERSLEY LAE 55322, Sept. 1972).

chous or perhaps slightly so, linear-lanceolate, the upper half curved forward, 0.5–0.8 mm wide. Leaves on older trees eventually becoming similar to the leaves of primary shoots but somewhat narrower and curved like the juvenile leaves, 2–5 by 0.4–0.6 mm, uniform along a shoot, often glaucous. *Pollen cone* sometimes on long shoots. *Involucral leaves* resembling the foliage leaves but curved throughout their length, completely surrounding the developing seed with its covering which rises slightly above them when mature, 6–10 mm long. Receptacle bright red when ripe. *Seed* with its covering 7 mm long and 6–7 mm diam.

Distr. *Malesia*: Central Celebes, Moluccas (Central Ceram: G. Binaja), and throughout New Guinea. Fig. 34.

Fig. 34. Range of *Dacrycarpus cinctus* (PILGER) DE LAUB.

Ecol. In New Guinea extremely common and often dominant, or co-dominant with *Nothofagus*, *Libocedrus*, *Elaeocarpus* and *Podocarpus*, in mountain forest and mossy forest, on Mt Binaja in orchard-like pure stands with a mossy ground cover, rarely in muddy parts of swamps (Iowasi swamp near Woitape), a canopy tree or sometimes emergent, often thick-trunked, the foliage glaucous or not, 1800–2850 m, occasionally as high as 3600 m, in Ceram from 1300–3000 m, in Celebes reported as low as 900 m.

Vern. Celebes: *sareh*, Upper Binuang, Ulu Sahu; New Guinea: *djasiha*, Asaro, Kefamo, *gu-gra-goin*, Goroka, Hagen lang., *jumbiri*, Mt Giluwe, Mendi lang., *kaiwilpitti*, Waghi, Minj, *kubil-kaibigl*, *kubuk-kajbek*, Kubor Ra., Minj, *kubin*, Hagen, Togoba, *ma-u*, Finisterre Ra., Naho lang., *pau*, Hagen-Wabag, Enga lang., *piepienie*, Mt Ne, Tari, Hula lang., *u(m)ba*, Chimbu lang. at various places.

Note. Collectors complain that this species grades into *D. compactus* and indeed in the zone of overlap between these two species specimens of *D. cinctus* have shorter and more robust leaves resembling *D. compactus*, while the common glaucousness of *D. cinctus* has been observed to disappear above 2950 m. The two species are substantially different, however, and both become much less common in the elevations where they overlap (2900–3400 m). Perhaps hybridization occurs where they overlap.

5. PRUMNOPITYS

PHILIPPI, Linnaea 30 (1860) 731; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 55; Blumea 24 (1978) 189. — *Stachycarpus* (ENDL.) TIEGH. Bull. Soc. Bot. Fr. 38 (1891) 162; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 81. — *Podocarpus sect. Taxoideae* BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 40. — *Podocarpus sect. Stachycarpus* ENDL. Syn. Conif. (1847) 218; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 399; PARL. in DC. Prod. 16, 2 (1868) 518; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 105; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 63; GIBBS, Ann. Bot. 26 (1912) 537; BUCHHOLZ & GRAY, J. Arn. Arb. 29 (1948) 58. — *Podocarpus sect. Prumnopitys* (PHILLIPPI) BERTRAND, Ann. Sc. Nat. V, 20 (1874) 65. — *Podocarpus subg. Stachycarpus* (ENDL.) ENGLER in E. & P. Nat. Pfl. Fam., Nachtr. 1 (1897) 21; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 242; WASSCHER, Blumea 4 (1941) 380. — **Fig. 36, 38, 39.**

For further synonyms see under section Sundacarpus.

Densely branched dioecious trees to 60 m tall. Bark smooth, fibrous, and reddish to yellowish brown, often darker on the surface but weathering to gray, on older trees breaking off in irregular more or less quadrangular plates 3–5 mm thick and 3–10 cm across, with scattered lenticel-like mounds. *Foliage buds* small and inconspicuous with overlapping triangular scales. *Leaves* spirally placed, bifacially flattened, linear, uninerved, without hypoderm, hypostomatic, narrowed at the decurrent base with a twist where the leaf leaves the stem so that the leaves appear distichous. *Pollen cones* axillary and solitary or grouped on scaly spike (or even compound structures). *Seed* with its covering solitary and subterminal or grouped along a scaly or leafy shoot, inverted and completely covered by a fleshy epimatium with an apical crest; the seed with a slightly asymmetrical ridge at the micropylar end.

Distr. 10 *spp.* in two slightly geographically overlapping sections, with the type section extending from Australia and New Caledonia to New Zealand and from Chile to Venezuela and Costa Rica. The monospecific section *Sundacarpus* is confined to *Malesia* and NE. Queensland. Fig. 35.

Uses. Several species are important timber trees.

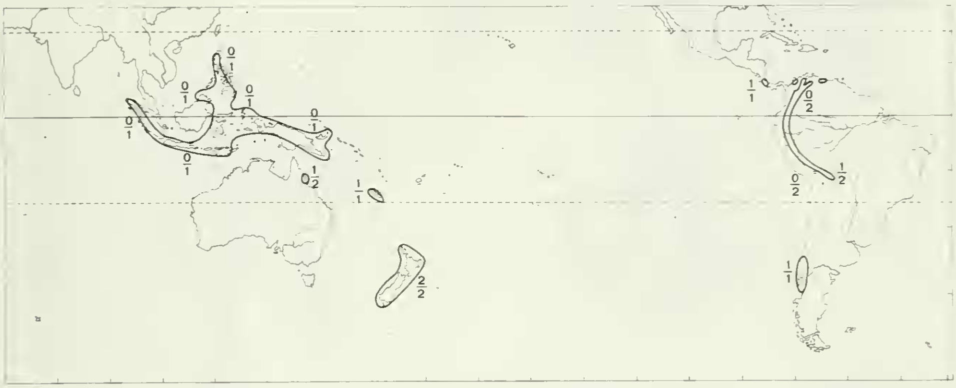

Fig. 35. Range of the genus *Prumnopitys* PHILIPPI. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

1. Section Sundacarpus

(BUCHHOLZ & GRAY) DE LAUB. Blumea 24 (1978) 190. — *Podocarpus sect. Sundacarpus* BUCHHOLZ & GRAY, J. Arn. Arb. 29 (1948) 57; FLORIN, Acta Horti Berg. 20 (4) (1963) 190, f. 20 (map). — *Stachycarpus sect. Sundacarpus* (BUCHHOLZ & GRAY) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 81.

1. Prumnopitys amara (BLUME) DE LAUB. Blumea 24 (1978) 190. — *Podocarpus amara* BLUME, En. Pl. Java 1 (1827) 88; BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 40; ENDL. Syn. Conif. (1847) 217; BLUME, Rumphia 3 (1849) 213, t. 170; MIQ. Fl. Ind. Bat. 6 (1859) 1073; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 395; DE BOER, Conif. Arch. Ind. (1866) 20; PARL. in DC. Prod. 16, 2 (1868) 516; BERTRAND, Ann. Sc. Nat. V, 20 (1874) 67; TIEGH. Bull. Soc. Bot. Fr. 38 (1891) 38; WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 68, f. 13A–D; K. & V. Bijdr. 10 (1904) 263; FOXW. Philip. J. Sc. 6 (1911) Bot. 159; KOORD. Exk. Fl. Java 1 (1911) 64, f. 1; HALL.*f.* Meded. Rijksherb. *n.* 14 (1912) 34; KOORD. Atlas 3 (1915) t. 590, 591; MERR. En. Philip. 1 (1922) 2; KOORD. Fl. Tjibodas (1922) 2; LANE-POOLE, For. Res. Terr. Papua & New Guinea (1925) 73; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245, f. 131A–D; WASSCHER, Blumea 4 (1941) 381; ORR, Trans. Bot. Soc. Edinb. 34 (1944) 11; GRAY & BUCHHOLZ, J. Arn. Arb. 32 (1951) 93; BACKER & BAKH.*f.* Fl. Java 1 (1963) 89. — *Podocarpus eurhyncha* MIQ. Fl. Ind. Bat. 2 (1856) 1074; DE BOER, Conif. Arch. Ind. (1866) 24, t. 3, f. 2; PARL.

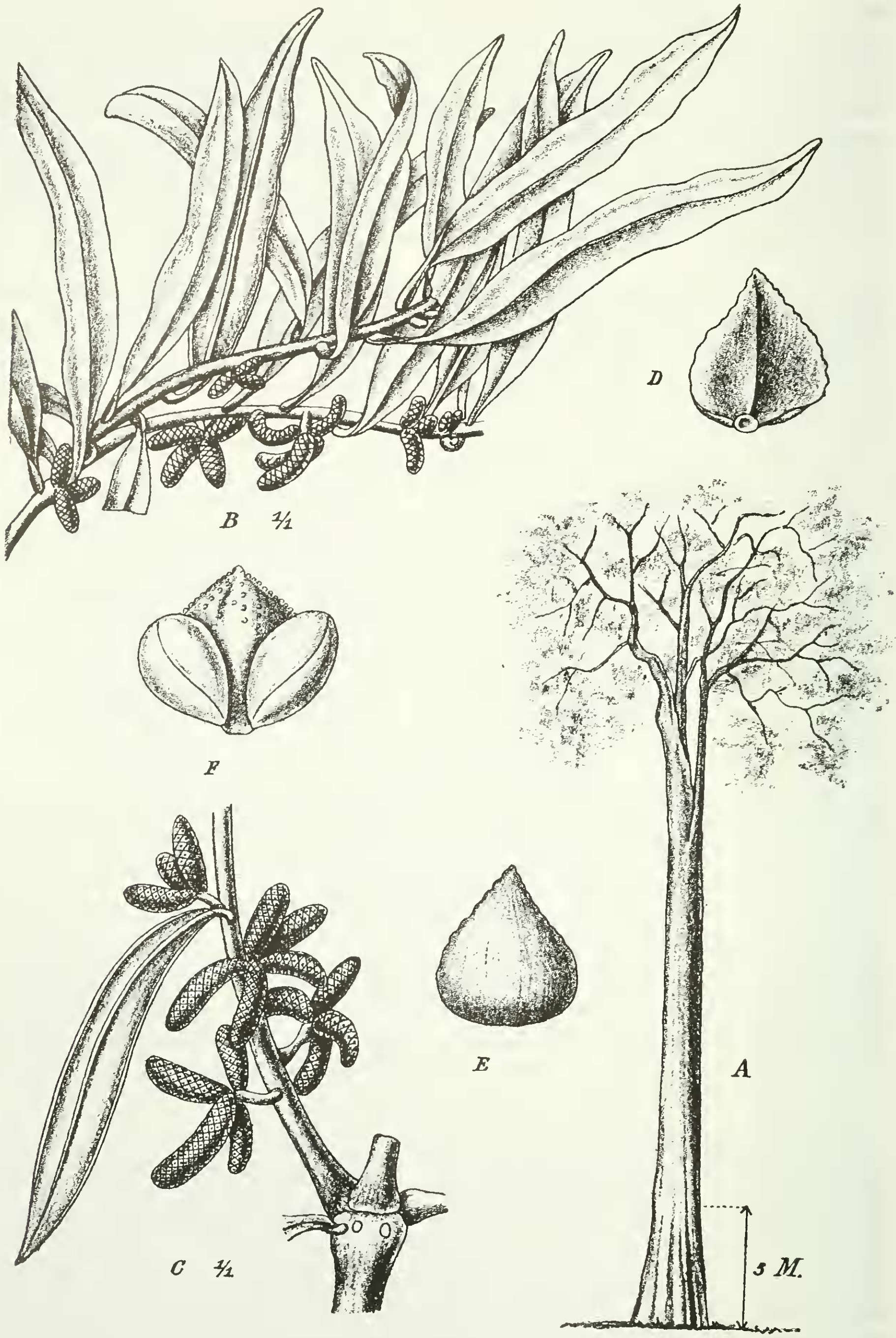

Fig. 36. *Prumnopitys amara* (BLUME) DE LAUB. A. Habit of tree; B, C. twigs with pollen cones; D–F. microsporophylls (different views) (from KOORD. Atlas 3, 1915, t. 590).

in DC. Prod. 16, 2 (1868) 518; WARB. Monsunia 1 (1900) 193. — *Podocarpus dulcamara* SEEM. Bonplandia 9 (1861) 253; *ibid.* 10 (1862) 365. — *Nageia amara* (BLUME) O. K. Rev. Gen. Pl. 2 (1891) 800. — *Nageia eurhyncha* (MIQ.) O. K. *l.c.* 800. — *Podocarpus pedunculata* BAILEY, Queensl. Agr. J. 5 (1899) 390, t. 144; Queensl. Fl. 5 (1902) 1498; BAKER & SMITH, Res. Pines Austr. (1910) 441; Hardwoods Austr. (1919) 429. — *Stachycarpus amara* GAUSSEN, Gymn. Act. & Foss. fasc. 12 (1973) f. 635, 646; *ibid.* 13, ch. 20 (1974) 105, f. 715 (map). — **Fig. 36, 38, 39.**

Tree 10–60 m high, 12–140 cm diam. Bark surface checkered by numerous cracks. Cotyledons 3 fused pairs. *Foliage buds* small, globose, with overlapping, rounded, keeled scales up to 2 mm long. *Juvenile leaves* oblong, 4–12 by up to 2 cm, more or less abruptly narrowing at the base to a 3–5 mm long petiole, narrowing abruptly at the apex to an elongated tapering 'drip tip' which is *c.* 2 mm wide and up to 20 mm long, apex rounded to acute. *Mature leaves* becoming longer and narrower, linear, narrowed at the base to a *c.* 5 mm long petiole, usually slightly acuminate and acute, a distinct groove over the midvein above, broadly raised below, 5–15 cm by 6–14 mm. *Pollen cones* 15–35 by 2.5–3.5 mm, solitary and terminal or grouped to at least seven on an auxillary 1–7 mm peduncle with several sterile basal scales. Apex of microsporophyll acute, triangular, keeled, *c.* 0.8 mm long. One to several *ovules* scattered laterally along a 3–5 mm scaly shoot, the scales triangular to rounded, decurrent, spreading, 1.5–2 mm long, the sterile scales deciduous. Ovule and its covering oval, longer than its bract (fertile scale) and distinctly crested at its apex, dark blue and glaucous. Growing *seed* and its covering elongated at both the micropylar end and the forwardly bent apex; mature seed and its covering nearly spherical, with a small obtuse crest, *c.* 25 mm diam., becoming reddish and then dark purple and glaucous. *Seed c.* 20 mm diam., with an indistinct ridge and minute apiculus formed from the micropyle, the smooth outer hard shell *c.* 1 mm thick, the fleshy covering *c.* 3 mm thick becoming wrinkled as it dries and often falling off.

Distr. NE. coastal Queensland; in *Malesia*: through and very common in New Guinea (incl. New Britain & New Ireland), Moluccas (Buru, Halmaheira, Morotai), Lesser Sunda Islands (Timor, Flores, West Sumbawa, Lombok), throughout Java, Central and SW. Celebes (Bonthain), Philippines (Mindanao, Luzon), Borneo (only in Sabah!), and Sumatra (Central–N., Batak region, rare in S. Palembang). Fig. 37.

Ecol. Scattered and often common in primary and secondary rain-forest, in New Guinea very common, often in Fagaceous forest, sometimes in mossy forest, in submontane forest at *c.* 900 m with *Dysoxylum*, *Macaranga*, *Ficus*, sometimes emergent as a colossal tree, often on latosols, rarely on sandy soils or on marshy ground, (sea-level–)500–2000(–2300) m, according to SMYTHIES (*in sched.*) to 3000 m in Sabah.

Fig. 37. Range of *Prumnopitys amara* (BLUME) DE LAUB.

A few times it is mentioned that the tree is buttressed (Pinosok Plateau and Mt Cyclops, New Guinea), or spurred, a rare feature in *Podocarpaceae.*

Uses. A fine timber tree, often of large dimension. In New Guinea mentioned to be used for joinery and furniture.

Vern. Sumatra: *kuta-béa, sitoba, sitobu*, Toba-Batak, *besi*, Karo-Batak, *buluh*, Pasemah, Palembang; Java: *ki bima, ki manang pait, ki marak, ki mèrak, ki pait, ki putri* (confusion with *Podocarpus neriifolius*), S; *tadji*, Tengger, *tjemoro*, Madiun (confusion with *Casuarina*), J; Borneo: *sempilau*, Kinabatangan; Lesser Sunda Islands: *pinis*, Flores, *kayu santen*, Batulante, Sumbawa; West New Guinea: *bublugie*, Wissel Lakes, Kapauko lang., *irbouska*, Manikiong, Ransiki, *du-on, nepa, niepa, nipah*, Kebar lang., *niwup*, Kebar Valley, Andjai dial., *tjermes*, Ransiki, Hattam lang.; East New Guinea: *kaibiltugl*, Wahgi, Minj, *kepim*, Pokaris, Wabag, Enga lang., *kumburum*, Mt Entaldam, Telefomin, *la-u*, Poget logging area, Wabag, *levekus*, Telefomin, *migimi*, Ogeramnang, *powa*, Pomagos R.C. Mission, Weng lang., *singai*, Bulolo, Garaina dial., *taso*, Wonatabe, *til*, Hagen, Togoba, *tsula*, Chimbu, Masul; New Britain: *nelil*, Mt Talawe. *Black pine*, Queensland.

Note. The leaves are variously reported as bitter ('amara'), to which also the Sundanese name 'pait' refers, bittersweet ('dulcamara'), or sweet tasting. This and the groove over the midvein most readily distinguishes it from similar-leaved associated *Podocarpus* species while the lack of hypoderm also gives a distinct texture to the leaves. The striking form of the juvenile leaves led to the description of *Podocarpus eurhyncha*. GRAY & BUCHHOLZ (1951) report that the leaves occasionally have a lateral pair of vascular resin canals in addition to the conspicuous central canal beneath the vascular bundle. Two collectors

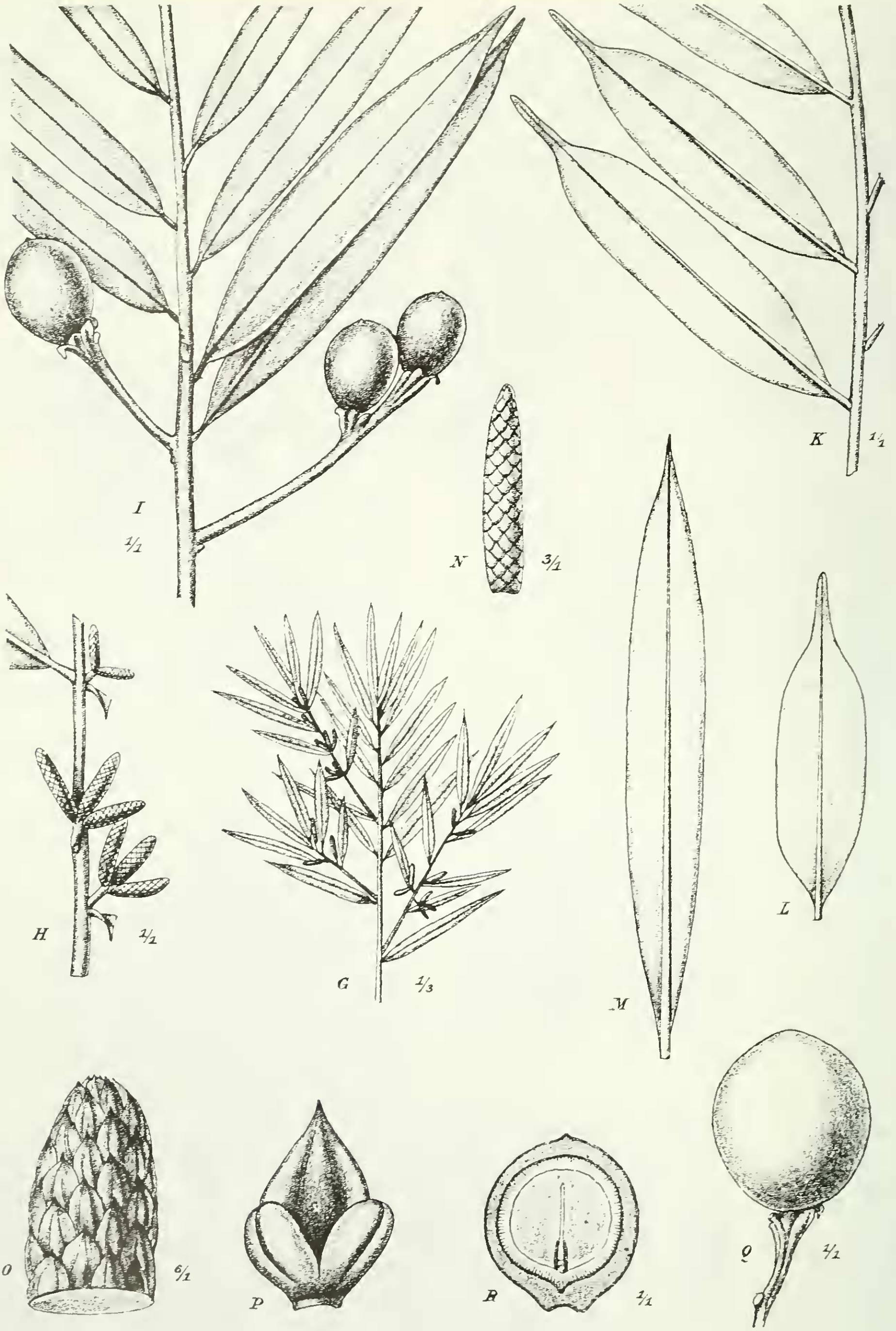

Fig. 38. *Prumnopitys amara* (BLUME) DE LAUB. G, H. Twigs with pollen cones; I. twig with seeds; K, L. twig and leaf of a young tree; M. leaf of an adult tree; N–P. pollen cones with details; Q, R. seed, also in cross section (from KOORD. Atlas 3, 1915, t. 591).

Fig. 39. *Prumnopitys amara* (BLUME) DE LAUB. Ripe seed red (Photogr. BW 2318).

report seeds with distinctive sculpturing on their surface but this is not evident in the corresponding preserved specimens. The normally three rather than two fused pairs of cotyledons is unique. The limited occurrence in Borneo is curious.

6. NAGEIA

GAERTN. De Fruct. & Sem. (1788) 191; GORDON, Pinetum (1858) 134; O. K. Rev. Gen. Pl. 2 (1891) 798; FLORIN, Acta Horti Berg. 20 (4) (1963) 190, f. 21 (map); DE LAUB. Blumea 32 (1987) 209. — *Decussocarpus* DE LAUB. J. Arn. Arb. 50 (1969) 340; Fl. Nouv. Caléd. et Dép. 4 (1972) 48; Kalikasan 7 (1978) 130. — **Fig. 41**.

Dioecious, erect shrubs or trees, 1–54 m tall. Bark tan to brown within and dark brown to black on the surface but often weathering to gray, peeling in irregular shaped plates to short vertical strips. *Leaves* opposite-decussate (or mixed with some leaves spirally placed), distinctly narrowed to a decurrent base. Juvenile leaves mostly larger than the adult leaves which are otherwise similar, twisted at the base so as to appear distichous, in most cases amphistomatic with the abaxial face uppermost on the left side of the shoot and the axial face uppermost on the right side (in a few species the leaves are hypostomatic and without this unique orientation). *Pollen cones* sessile or terminal, solitary or grouped, cylindrical (or oval). Each inverted *seed* completely covered by the fertile scale (epimatium), one or occasionally two subterminal on a scaly shoot, the usually persistent leathery covering becoming more or less fleshy when ripe.

Distr. There are 12 *spp.* in the three sections through most of the tropical forests of the world, throughout *Malesia*, where two sections overlap each other. Fig. 40.

KEY TO THE SECTIONS

1. Leaves large, broad, ovate to broad-lanceolate, with many longitudinal veins .... **1.** *Sect.* **Nageia**
1. Leaves small, with a single rib .... **2.** *Sect.* **Polypodiopsis**

1. Section Nageia

DE LAUB. Blumea 32 (1987) 209. — *Podocarpus sect. Dammaroides* BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 41. — *Podocarpus sect. Nageia* ENDL. Syn. Conif. (1847) 207; MIQ. Fl. Ind. Bat. 2 (1859) 1071; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 378; DE BOER, Conif. Arch. Ind. (1866) 12; PARL. in DC. Prod. 16, 2 (1868) 507; BERTRAND, Ann. Sc. Nat. V, 20 (1874) 66; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 59; GIBBS, Ann. Bot. 26 (1912) 533; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 242; WASSCHER, Blumea 4 (1941) 415; BUCHHOLZ & GRAY, J. Arn. Arb. 29 (1948) 56; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 11. — *Decussocarpus sect. Dammaroides* (BENNETT) DE LAUB. J. Arn. Arb. 50 (1969) 348; Kalikasan 7 (1978) 130.

Erect shrubs or trees, 1–48 m tall. Bark smooth, on trees peeling in large thin irregular shaped plates with scattered lenticels. *Foliage buds* a compact cluster of lanceolate deciduous scales abruptly wider than the shoot and distinctly acute, when terminal often 2–3 mm beyond the last leaf bases, 3–6 mm long, lateral buds sessile. Primary shoots not differentiated from ultimate shoots. *Leaves* with many parallel vascular bundles (one of which is medial) converging towards the acute to acuminate apex, more or less elliptic but juvenile leaves very acuminate and adult leaves sometimes more or less blunt, distichous, amphistomatic with equal basal twists (or hypostomatic with opposite basal twists), narrowed to a short broad petiole. *Fertile shoots* arising in the axils of leaves from sessile buds essentially the same as foliage buds, one to several pairs of deciduous scales below the first pollen cone or the female receptacle. *Pollen cones* cylindrical, solitary or grouped with one terminal and others forming sessile decussate pairs about 5 mm apart, each cone in the axil of a sterile scale but the terminal three often fused at their bases. In some species a part of the fruit-bearing shoot becoming enlarged and eventually fleshy forming a receptacle, otherwise a part of the shoot often remaining attached to the seed when it falls. *Seed* smooth, nearly spherical but elongated on the micropylar end into a small asymmetrical beak.

Distr. There are 5 *spp.* from southern India and Bangladesh across Indochina and Malesia to New Britain and through southern China to southern Japan; in *Malesia* 3 *spp.* Fig. 40.

Notes. Sterile specimens often confused with *Agathis* with very similar leaves, but in *Agathis* the parallel vascular bundles do not markedly converge towards the leaf apex and the terminal bud is globular, not acute, but very blunt-rounded.

The key to the three species is inadequate for identification of sterile material, but the leaf-size and length of the petiole may be helpful, though sizes overlap.

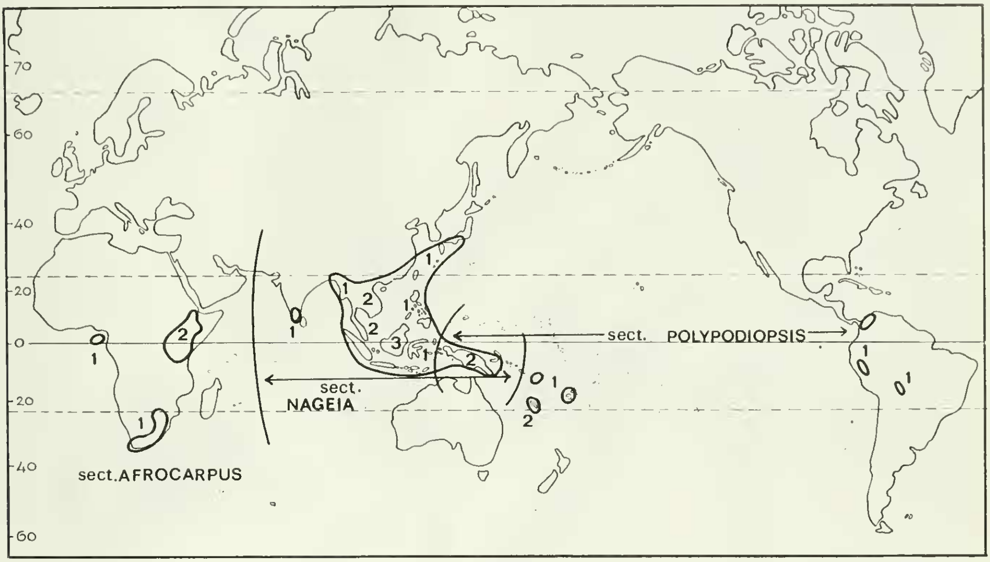

Fig. 40. Range of the genus *Nageia* GAERTN. and its three sections, with the number of species.

KEY TO THE SPECIES

1. Fruit with fleshy receptacle.
 2. Pollen cones grouped on a peduncle. Leaves at least 6 cm long .... **1. N. wallichiana**
 2. Pollen cones solitary, sessile. Leaves mostly less than 5 cm long .... **2. N. motleyi**
1. Fruit lacking a fleshy receptacle. Large-leaved .... **3. N. maximus**

1. Nageia wallichiana (PRESL) O. K. Rev. Gen. Pl. 2 (1891) 800; DE LAUB. Blumea 32 (1987) 210. — *Podocarpus latifolius* (*non* THUNB. 1794) BLUME, En. Pl. Jav. 1 (1827) 89; WALL. Pl. As. Rar. (1830) 26; HORSFIELD in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 41; LOUDON, Arb. & Fruct. Brit. 4 (1838) 2100, f. 1995; HASSK. Cat. Hort. Bog. (1844) 70; ENDL. Syn. Conif. (1847) 208; MIQ. Pl. Jungh. 1 (1851) 1; Fl. Ind. Bat. 2 (1859) 1071; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 379; DE BOER, Conif. Arch. Ind. (1866) 12; PARL. in DC. Prod. 16, 2 (1868) 508; HOOK.*f.* Fl. Brit. India 5 (1896) 649. — *Podocarpus wallichianus* PRESL, Bot. Bemerk. (1844) 110; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 59; RIDLEY, J. Str. Br. R. As. Soc. *n.* 60 (1911) 57; HICKEL, Fl. Gén. I.-C. 5 (1931) 1068; KENG in Whitmore, Tree Fl. Malaya 1 (1972) 53, f. 5d–f; PHENGKLAI, Thai For. Bull. Bot. 7 (1973) 17, f. 11; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 18. — *Podocarpus blumei* ENDL. Syn. Conif. (1847) 208; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 380; PARL. in DC. Prod. 16, 2 (1868) 508; BECC. Malesia 1 (1877) 178; WARB. Monsunia 1 (1900) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 60, t. 9; K. & V. Bijdr. 10 (1904) 261; KOORD. Exk. Fl. Java 1 (1911) 67; FOXW. Philip. J. Sc. 6 (1911) Bot. 158, t. 28, f. 2; KOORD. Atlas 3 (1915) f. 588; RIDLEY, Fl. Mal. Pen. 5 (1925) 281; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245, t. 134B; Bot. Jahrb. 68 (1937) 245; CORNER, Wayside Trees (1940) 717; WASSCHER, Blumea 4 (1941) 416; BACKER & BAKH.*f.* Fl. Java 1 (1963) 89; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 20, f. 736. — *Podocarpus agathifolia* BLUME, Rumphia 3 (1849) 217, t. 173. —

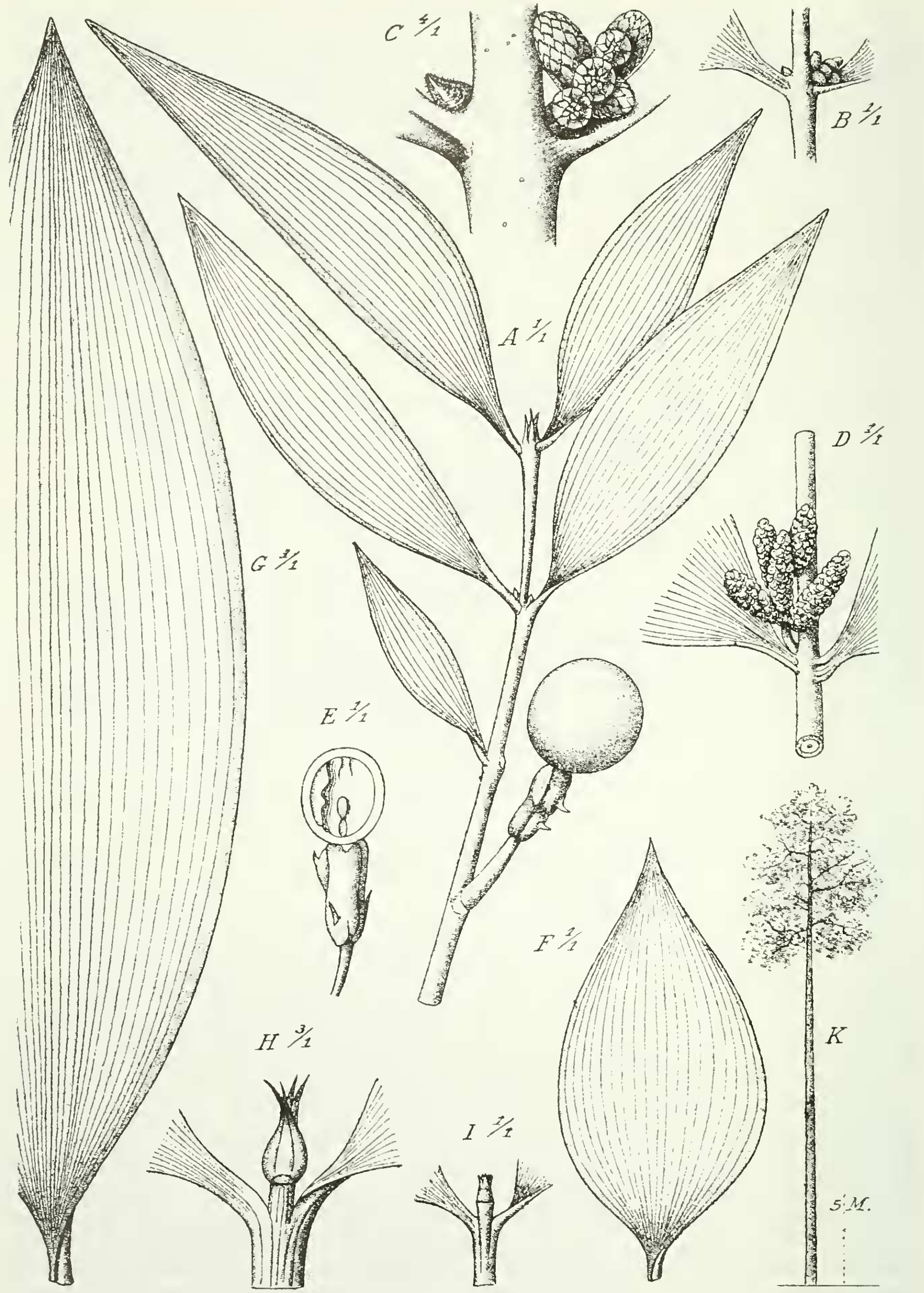

Fig. 41. *Nageia wallichiana* (PRESL) O.K. A. Twig with seed; B, C. twig portion with young pollen cones; D. *ditto* with mature pollen cones; E. longitudinal section of seed; F. leaf of a mature tree; G. leaf of a young tree; H, I. terminal foliage buds; K. habit of tree (from KOORD. Atlas 3, 1915, t. 588).

N. blumei (ENDL.) GORDON, Pinetum (1858) 138. — *Podocarpus latifolia f. ternatensis* DE BOER, Conif. Arch. Ind. (1866) 14. — *Decussocarpus wallichianus* (PRESL) DE LAUB. J. Arn. Arb. 50 (1969) 349; Kalikasan 7 (1978) 131. — Fig. 41.

Tree, 10–54 m high, 7–60 cm diam., clear bole to 30 m. *Leaves* quite variable both on juvenile and adult plants with the larger leaves growing in the shade, 6–14(–23) by 2–5(–9) cm, 2 to at least 6 times as long as broad; petiole 5–10 mm. *Pollen cones* in groups of up to at least 7 on a 2–10 mm peduncle; mature cone 8–18 by 3–4 mm. Apex of the microsporophyll lanceolate, 2–3 mm long. *Seed-bearing structure* solitary on a 8 to at least 20 mm peduncle with caducous scales or occasionally reduced leaves. *Receptacle* with 4–7 sterile, deflexed, slightly enlarged bracts, 7–18 mm long before becoming ripe and fleshy, dark purple or black when ripe. *Seed* with its covering 15–18 mm diam.

Distr. Southeast Asia (S. extremity of the Deccan Peninsula, Assam, Burma, Thailand, Indochina, Yunnan); in *Malesia*: Sumatra, Malaya, Banka I., W. Java, Lesser Sunda Islands (Flores), Borneo (incl. Karimata I.), Philippines (Luzon, Sibuyan, Mindoro, Panay, Samar), N. & Central Celebes, Moluccas (Obi, Ternate, Morotai, Ceram), New Guinea (incl. Meos Num, Biak, Japen, and Normanby Is.). Fig. 42.

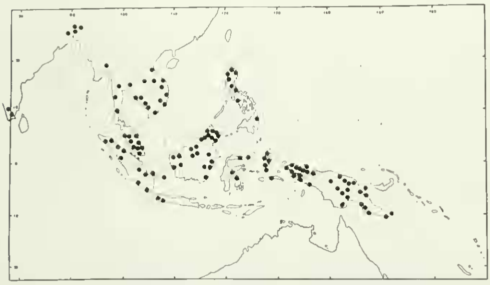

Fig. 42. Range of *Nageia wallichiana* (PRESL) O.K.

Ecol. Scattered and often common in primary rain-forests, nowhere reported gregarious or dominant, from very low elevation (5 m) ascending occasionally as high as 2100 m.

Collected in peat-swamps in Sumatra and Borneo, or dry parts of them, in the lowland, in Sarawak on basalt ridges and submontane kerangas, in E. Borneo (G. Beratus) in mossy forest on sandstone, in Sabah in sandy pelawan (*Tristania*) forest, in New Guinea on clay or sandy ridge forest, sometimes associated at submontane altitude with *Anisoptera, Cinnamomum, Sloanea, Castanopsis*, or with *Araucaria-Podocarpus-Fagaceae* at 700 m. In Thailand buttresses are recorded, at Arguni Bay (New Guinea) even high buttresses; this seems to occur occasionally.

Uses. The tree yields a good timber. In Obi planks are used for house construction. In the Fly R. area it is used for smaller canoe logs.

Vern. Malaya: *podo kebal musang gunong*; Sumatra: *kayu bulu soma*, Asahan, Batak lang., *labu rimba*, Sibolga, *lanang*, Pasamah, Palembang, *medang sepaling*, Bencoolen, *setebal*, Banjumasin, Palembang, *sibulu somak*, Simelungun; W. Java: *ki bima, ki putri*, S; Borneo: *kebal musang*, Tawau, *manggilan*, Tambunan, Dusun lang., *mengilan*, Sabah, Serudong, *salung puteh*, Merurong Plateau; Philippines: *mala almaciga*, Tag.; Celebes: *molosambongé = tombolilato*, Buladu, N. Cel., *tandangguli*, Malili; Lesser Sunda Islands: *tilu tuna*, Flores; Moluccas: *damar laki laki*, Obi; West New Guinea: *augom(m)a*, Wariki, Manikiong lang., *bararang*, Meos Num, Pom lang., *kabeirefo*, Tiwara, Irahutu lang., *mangurif*, Biak lang., *mejerka*, Sidai, Arfak Sidai dial., *misorvira*, Tairi, Borowai lang., *mop*, Mandobo lang., *mungkas*, Beriat, Tehid lang., *neusuwierie*, Esania lang., *nibwau*, Kebar Valley, Andjai dial., *nipa*, Kebar lang., *niwob*, Kebar dial., *manakasap*, Japen, Sambar lang., *nidjet*, Sidai, Amberbaken lang., *orsonkobu*, Warsamson, Mooi lang., *waramira*, Mimika, *wok*, Muju lang.; East New Guinea: *durwe*, Wagu, *mewango, mewongo*, Maipa village, Mekeo lang., *ososo biri biri*, Oomsis, *waswayangumi*, Waskuk.

2. Nageia motleyi (PARL.) DE LAUB. Blumea 32 (1987) 210. — *Dammara motleyi* PARL. En. Sem. Hort. Bot. Mus. Florent. (1862) 26; SEEM. J. Bot. 1 (1863) 36; PARL. in DC. Prod. 16, 2 (1868) 377. — *Podocarpus beccarii* PARL. in DC. Prod. 16, 2 (1868) 508; WARB. Monsunia 1 (1900) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 59. — *N. beccarii* (PARL.) GORDON, Pinetum ed. 2 (1875) 186. — *Agathis motleyi* (PARL.) WARB. Monsunia 1 (1900) 185. — *Podocarpus motleyi* (PARL.) DÜMMER, J. Bot. 52 (1914) 240; WASSCHER, Blumea 4 (1941) 421, t. 4, f. 11; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 22, f. 737; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 51, f. 5. — *Decussocarpus motleyi* (PARL.) DE LAUB. J. Arn. Arb. 50 (1969) 352.

Tree to 54 m high. *Leaves* 3–5(–7.5) by 1.5–2.2 (–2.8) cm, 1.5–3 times as long as broad; petiole 2–3 mm. *Pollen cones* solitary and sessile in the leaf axils, 15–20 by 5–6 mm. Apex of microsporophylls lanceolate to acuminate, at least 2 mm long. *Seed-bearing structure* solitary on a scaly 2–5 mm peduncle. *Receptacle* with 5–9 sterile, spreading, slightly enlarged bracts, 8–12 mm long before becoming ripe and fleshy. *Seed* with its covering 13–16 mm diam.

Distr. Southernmost Thailand; in *Malesia*: Ma-

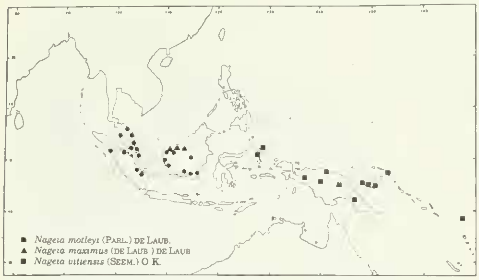

Fig. 43. Range of three species of *Nageia*.

laya, throughout Sumatra and Borneo (Sarawak & SE. Borneo). Fig. 43.

Ecol. Scattered in primary and secondary rainforest, from very low altitude (15 m) to *c.* 500 m. It occurs on slopes and hills on dry soil, but also in Borneo in two different situations: in Sarawak it is collected on deep peat in a mixed *ramin*-peat swamp, but also on ridges and hillsides in *bindang*-dipterocarp forest and at Lawas at 1000 m on podsolic sandy loam.

Vern. Malaya: *podo kebal musang*; Sumatra: *kayu bawa, setebal*, Palembang; Sarawak: *medang buloh*, Simunjan.

3. **Nageia maximus** (DE LAUB.) DE LAUB. Blumea 32 (1987) 210. — *Decussocarpus maximus* DE LAUB. J. Arn. Arb. 50 (1969) 353. — *Podocarpus maximus* (DE LAUB.) GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 14, f. 742.

Erect shrub to tree, 1–10 m high. *Leaves* (8–) 16–34 by (3–)6–9.5 cm, acuminate, 2.5–3.5 times as long as broad; petiole 4–10 mm. *Pollen cones* in groups of up to 9 on a 3–10 mm peduncle, 12–20 by 2.5–3 mm. Apex of microsporophyll more or less lanceolate, 0.5–1 mm long. *Seed-bearing structure* solitary or grouped to as many as five on a scaly shoot *c.* 6 mm long, the individual peduncles up to 12 mm long, not forming a fleshy receptacle. *Seed* and its cover 16–18 mm diam.

Distr. *Malesia*: Borneo (Sarawak, very local), a few collections. Fig. 43.

Ecol. Locally common in the understory of moist rain-forest on ridge in Bako National Park and in peat-swamp forest, from near sea-level to 120 m.

Vern. *Landin paya*, Naman For. Res.

2. Section Polypodiopsis

(BERTRAND) DE LAUB. Blumea 32 (1987) 210. — *Podocarpus sect. Polypodiopsis* BERTRAND, Ann. Sc. Nat. V, 20 (1874) 65; WASSCHER, Blumea 4 (1941) 423; BUCHHOLZ & GRAY, J. Arn. Arb. 29 (1948) 57; GRAY, *ibid.* 43 (1962) 67; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 27. — *Decussocarpus sect. Decussocarpus* DE LAUB. J. Arn. Arb. 50 (1969) 341.

Erect shrubs or trees, 2–43 m high. Foliage buds a loose cluster of rounded scales; at the apex of foliage shoots not destined to continue growth there are found only a few very reduced leaves. *Leaves* with a single vascular bundle, lanceolate, oval to nearly linear, acute or rounded at the apex, less than 5 times as long as wide, amphistomatic, distichous when juvenile and adult (adult leaves sometimes not distichous), sessile or with a very short petiole. A part of the not fleshy fertile shoot remaining attached to the seed and its covering when it falls. *Seed* ovate or globular with an elongated beak at the micropylar end.

Distr. There are 5 *spp.* from the Moluccas across New Guinea to Fiji and from Peru and western Brazil to Venezuela. Fossils have been reported from southern Australia, New Zealand, and S. Chile [FLORIN, Acta Horti Berg. 20 (4) (1963)]. One species in *Malesia*. Fig. 40.

4. **Nageia vitiensis** (SEEM.) O. K. Rev. Gen. Pl. 2 (1891) 800; DE LAUB. Blumea 32 (1987) 210. — *Podocarpus vitiensis* SEEM. Bonplandia 10 (1862) 366; J. Bot. 1 (1863) 33, t. 11; Fl. Vitiensis (1868) 266, t. 78; TIEGH. Bull. Soc. Bot. Fr. 38 (1891) 169; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 63; GIBBS, J. Linn. Soc. Bot. 39 (1909) 182; Ann. Bot. 26 (1912) 533, t. 49, f. 14–16, t. 50, f. 17–18, t. 53, f. 72–73; STILES, Ann. Bot. 26 (1912) 533; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245; WASSCHER, Blumea 4 (1941) 425; GRAY, J. Arn. Arb. 43 (1962) 72; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 38, f. 747. —

Podocarpus filicifolius GRAY, J. Arn. Arb. 43 (1962) 74, *p.p.*; DE LAUB. Blumea 15 (1967) 440; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 40. — *Decussocarpus vitiensis* (SEEM.) DE LAUB. J. Arn. Arb. 50 (1969) 342.

Tree, 12–43 m high, up to 50–130 cm diam. Bark smooth, peeling in thin plates. Primary shoots with thin dispersed decussate rounded deciduous scales 1–2 mm long and broadly decurrent. *Foliage shoots* lateral or terminal with leaves somewhat smaller towards the extremities and a few very reduced leaves or scales at the base, usually not continuing growth after a resting period but sometimes producing a second cycle of growth or sometimes converting to a primary shoot. *Leaves* distichous, narrowed abruptly at the twisted base, broadly decurrent, linear-lanceolate to ovate, blunt, an indistinct rib marking the midvein on either surface, juvenile leaves up to 40 by 8 mm and consistently lanceolate, adult leaves 15–25 by 3–5 mm. *Pollen cones* subtended by a few crowded sterile scales similar to but smaller than those of the primary shoots, occasionally solitary in the axils of leaves but usually at the base of a foliage shoot or the upper portion of primary shoots, solitary or clustered (with one terminal) on scaly shoots or sometimes compound clusters, ovate when immature but elongating upon maturity and cylindrical, 12–24 by 2–2.5 mm. Apex of the microsporophylls triangular, at least 1 mm long. *Ovuliferous shoot* solitary in positions similar to the pollen cones, 6–10 mm long, scaly with the subterminal fertile scale or scales slightly larger. *Seed* with its covering globular but elongated into a curved beak towards the micropylar end which lies close to the attachment of the seed to the fertile shoot, the other (distal) end with a small crest which may persist on the mature seed whose coat becomes deep red and fleshy when ripe. *Seed* itself blunt on the base, 13–16 mm long including the beak, 8–10 mm diam.

Distr. Fiji Is., Solomon Is. (Santa Cruz group); in *Malesia*: throughout New Guinea (incl. New Britain) and the Moluccas (Morotai). Fig. 43.

Ecol. Scattered and locally common in montane rain-forest, near the Wissel Lakes common, in New Britain co-dominant with *Gymnostoma*, in New Guinea sometimes frequent in *Agathis-Quercus* rainforest, from sea-level up to 1800 m.

Uses. In Fiji a valuable timber tree.

Vern. *Mugo*, Wissel Lakes, Kapauko lang., *lehil*, Mt Tangis, New Britain.

Note. The stem is at the base sometimes recorded as fluted or spur-buttressed. HENTY (*in sched.*) found the leaves and bark aromatic.

7. PODOCARPUS

L'HÉRIT. *ex* PERSOON, Synops. 2 (1807) 580, *nom. cons., non* LABILL. (1806); ENDL. Gen. Pl. *n.*1800 (1810); L.C. & A. RICH. Comm. Bot. Conif. & Cycad. (1826) 124; BLUME, En. Pl. Jav. 1 (1827) 88; BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 35; ENDL. Syn. Conif. (1847) 206; BLUME, Rumphia 3 (1849) 212; MIQ. Fl. Ind. Bat. 2 (1859) 1071; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 377; DE BOER, Conif. Arch. Ind. (1866) 12; PARL. in DC. Prod. 16, 2 (1868) 507; BENTH. & HOOK. *f.* Gen. Pl. III, 1 (1880) 434; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 104; BEISSNER, Nadelholzk. (1891) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 54; K & V. Bijdr. 10 (1904) 259; PILGER in E. & P. Nat. Pfl. Fam., Nachtr. 3 (1908) 4; KOORD. Exk. Fl. Java 1 (1911) 63; RIDLEY, J. Str. Br. R. As. Soc. *n.* 60 (1911) 56; FOXW. Philip. J. Sc. 6 (1911) Bot. 155; KOORD. Fl. Tjibodas (1918) 2; RIDLEY, Fl. Mal. Pen. 5 (1925) 280; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 240; WASSCHER, Blumea 4 (1941) 360; BUCHHOLZ & GRAY, J. Arn. Arb. 29 (1948) 54; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 59; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 3; DE LAUB. Kalikasan 7 (1978) 133; Blumea 30 (1985) 251. — **Fig. 46, 62.**

Usually dioecious shrubs to large trees up to 45 m tall. Yellowish to reddish brown soft fibrous bark weathering to gray, more or less fissured and peeling in short to long vertical strips. Vigorous branching of the primary stem tends to produce false whorls, otherwise branching is less regular to irregular. *Growth* is by flushes with new leaves sometimes distinctly red rather than the more common shades of lighter green. Distinct resting buds are formed at the apex of each leafy shoot and consist of two kinds of usually deciduous scales. *Primary scales* which cover the resting shoot apex are produced in a cluster of 4 or 5 generally unequal, keeled, mostly acute, triangular to lanceolate, partly overlapping scales, mostly 1.5–2 mm wide at the base, the width related to the vigour of the shoot. *Secondary scales* surround the newly growing shoot and are broader, membranous, and blunt to acuminate. The growth and emergence of the secondary bud can produce striking changes in the appearance of the foliage bud. On vigorous shoots the foliage bud is typically *c.* 4 mm diam., while weaker shoots have buds 2–3 mm diam., but larger or smaller buds characterize certain sections of the genus. *Leaves* spirally placed, bifacially flattened, uninerved, the midrib flat or prominent, either with a distinct hypoderm or well developed accessory transfusion tissue but mostly with both, hypostomatic, or rarely with a few upper stomata, more or less narrowed at the base into a short petiole. *Pollen cones* produced in an axillary or occasionally terminal structure corresponding to a foliage shoot. The primary pollen cone bud is sessile or produced on a short naked peduncle and consists of 3 (4) small, more or less equal scales and appears usually concurrently with the development of foliage buds which it resembles, but is usually somewhat smaller with the individual scales typically *c.* 1 mm wide at the base (wider in some sections). One or more cylindrical pollen cones typically *c.* 25 mm long emerge from the primary bud simultaneously with the elongation of the secondary foliage buds, each pollen cone developing from a secondary bud which resembles the secondary foliage bud (which, however, is always solitary within the primary foliage bud). The typical pollen cone is up to 4 mm diam. before the elongation which accompanies pollen shedding and 2.5–3.5 mm diam. after shedding. In a few species the scaly base of the pollen cone also elongates along with the fertile part at anthesis. The whole male structure falls as soon as the pollen is shed, the basal scales usually not falling separately. The *seed-bearing structure* is axillary mostly on new foliage shoots and consists of a naked peduncle commonly *c.* 5–15 mm long surmounted by two (to five) thickened adnate bracts which form a *receptacle* typically 7–12 mm long which in most species becomes fleshy and greatly enlarged upon maturity, one or more of the bracts in a subterminal position may be fertile. The inverted *ovule* is completely enclosed in the leathery epimatium which often forms a crest at the distal end where it folds over the base of the ovule and the resulting structure is completely exposed above the receptacle. The *seed* is usually glaucous when immature and more or less green when mature (rarely with the seed cover becoming fleshy or flushed with red), the seed cover normally persistent even after drying.

Distr. There are two slightly overlapping subgenera with 95 *spp.* across the lower and southern latitudes, throughout the southern temperate forests, all of the tropical highland forests, and throughout the Asian–Malesian tropical lowland forests with a few species reaching other tropical lowlands and others the Asian subtropics. In *Malesia* only *subg. Foliolatus* is represented. Fig. 44.

Fig. 44. Range of the genus *Podocarpus* L'HÉRIT. *ex* PERSOON. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

Subgenus Foliolatus

DE LAUB. Blumea 30 (1985) 263.

Receptacle with two subtending foliola (lanceolate bracts); stomata without a 'Florin ring' (BUCHHOLZ & GRAY, 1948); leaves with accessory transfusion tissue, never with resin canals at the leaf margins but in most cases at least three resin canals below or beside the vascular bundle; in most cases a ridge over the vascular bundle on the upper leaf surface, never a channel; juvenile leaves generally similar to adult leaves. Female receptacle becoming fleshy when mature but seed cover remaining leathery and greenish.

Distr. From Central China and Japan to eastern Nepal, across all of *Malesia* to eastern Australia and Tonga 53 *spp.* in 9 mostly overlapping sections. In *Malesia*: 8 sections with 30 *spp.*

KEY TO THE SECTIONS

1. Pollen cones solitary or in groups of 3 or fewer.
  2. Pollen cones regularly in threes or a mixture of threes and fewer (pollen cones usually at least 2.5 mm diam.; midrib more than 0.3 mm wide; ripe receptacle usually red).
    3. Primary foliage budscales erect and free, secondary budscales acute to acuminate.
      4. Secondary budscales broadly acute, primary budscales generally less than four times as long as broad; adult leaves not acuminate, usually not abruptly expanded at the base. *Spp.* 1–8 **1.** *Sect.* **Foliolatus**
      4. Secondary budscales acuminate, primary budscales more than four times as long as broad; adult leaves acuminate, abruptly expanded at the base. *Spp.* 9–10 .... **2.** *Sect.* **Acuminatus**
    3. Primary foliage budscales imbricate, forming a globular ball; secondary budscales blunt. *Spp.* 11–12 **3.** *Sect.* **Globulus**

2. Pollen cones normally solitary (only rarely grouped) (external budscales erect and free; leaves not at all acuminate).
  5. Foliage buds much longer than wide (with long lanceolate scales), secondary budscales acuminate. Bracts below the receptacle usually at least 3 mm long (ripe receptacle, red). *Spp.* 13–17 ..... 4. *Sect.* **Longifoliolatus**
  5. Foliage buds less than twice as long as wide, secondary budscales not acuminate. Bracts below the receptacle usually less than 2.5 mm long (midrib less than 0.3 mm wide).
    6. Pollen cones less than 3 mm diam., apex of the microsporophyll less than 0.5 mm long. Foliage bud less than 2 mm diam. *Spp.* 18–21 ..... 5. *Sect.* **Gracilis**
    6. Pollen cones more than 3.5 mm diam., apex of the microsporophyll more than 1 mm long. Foliage bud mostly more than 2 mm diam. Ripe receptacle usually purple or black. *Spp.* 22–25. ..... 6. *Sect.* **Macrostachyus**

1. Pollen cones regularly in clusters of more than 3.
  7. Outer budscales imbricate, apex of the scales slightly if at all raised. Midrib on the upper side of the leaf broad and flat. Ripe receptacle red. *Spp.* 26–27 ..... 7. *Sect.* **Rumphius**
  7. Outer budscales erect and free. Midrib narrow and in most species prominently raised. Ripe receptacle usually purple. *Spp.* 28–30 ..... 8. *Sect.* **Polystachyus**

VEGETATIVE KEY TO THE SECTIONS

1. Primary budscales imbricate, forming a ball or pyramid with few or none of their apices raised, bud no longer than diameter.
  2. Primary budscales overlapping and forming a ball or in some cases meeting pyramid-like at the bud apex but the scale apices never recurved outward; leaf hypoderm absent or occasionally slightly developed; leaf midvein generally more than half a mm wide but never a full mm ..... 3. *Sect.* **Globulus**
  2. Primary budscales mostly in the form of a pyramid with usually one or more scales recurved outward at the apex; leaves with continuous upper hypoderm and well developed lower hypoderm; leaf midvein more or less one mm wide ..... 7. *Sect.* **Rumphius**

1. Primary budscales with completely free apices, bud usually longer than diameter.
  3. Adult leaves distinctly acuminate; primary budscales mostly more than four times as long as wide ..... 2. *Sect.* **Acuminatus**
  3. Adult leaves not acuminate but where transitional leaves may be slightly acuminate, the primary budscales less than four times as long as wide.
    4. Foliage buds at least twice as long and generally much longer than basal diameter (leaves not at all acuminate).
      5. Leaves lanceolate, widest near the base.
        6. Midrib on upper side of leaf at least 0.2 mm high, often prominent ..... 4. *Sect.* **Longifoliolatus**
        6. Midrib on upper side of leaf less than 0.2 mm high, indistinct... 8. *Sect.* **Polystachyus** (*P. ridleyi*)
      5. Leaves more or less linear, not widest near the base (buds only sometimes more than twice as long as basal diameter).
        7. Leaves less than 7 mm wide, 5 cm long, midrib on the upper side less than 0.2 mm high ..... 4. *Sect.* **Longifoliolatus** (*P. gibbsii*)
        7. Leaves at least 8 mm wide, 4 cm long, midrib on upper side *c.* 0.3 mm high ..... 1. *Sect.* **Foliolatus** (*P. borneensis*)
    4. Foliage buds less than twice as long as basal diameter.
      8. Basal diameter of foliage bud 1–2 mm (midrib on upper side of leaf 0.2 mm high and less than 0.5 mm wide).
        9. Midrib on upper side of leaf 0.2 mm wide ..... 5. *Sect.* **Gracilis**
        9. Midrib on upper side of leaf at least 0.3 mm wide ..... 8. *Sect.* **Polystachyus**
      8. Basal diameter of foliage bud at least 2 mm, usually considerably more.
        10. Midrib on upper side of leaf less than 0.2 mm high and 0.7 mm wide.
          11. Leaf midrib 0.2–0.3 mm wide ..... 6. *Sect.* **Macrostachyus**
          11. Leaf midrib at least 0.5 mm wide.
            12. Leaf less than 7 mm wide, 5 cm long; basal diameter of foliage bud less than 3 mm; leaf midrib 0.5–0.7 mm wide, distinct ..... 4. *Sect.* **Longifoliolatus** (*P. gibbsii*)
            12. Leaf at least 8 mm wide, 5 cm long; basal diameter of foliage bud 3–4 mm (*P. levis*) or leaf midrib broad and indistinct (*P. spathoides*) ..... 1. *Sect.* **Foliolatus**

10. Midrib on upper side of leaf at least 0.2 mm high and 0.3 mm wide but where less than 0.5 mm wide it is at least 0.3 mm high.
13. Leaf midrib at least 0.3 mm high .... 1. *Sect.* **Foliolatus**
13. Leaf midrib 0.2–0.3 mm high.
14. Leaf midrib 0.5–0.6 mm wide .... 8. *Sect.* **Polystachyus** (*P. macrocarpus*)
14. Leaf midrib 0.8–1.2 mm wide .... 7. *Sect.* **Rumphius** (*P. laubenfelsii*)

1. Section Foliolatus

DE LAUB. Blumea 30 (1985) 264.

Primary foliage budscales erect, triangular to shortly lanceolate; secondary scales acute, the secondary bud when it first appears generally a pyramid whose apex is formed of a cluster of crowded scale tips. *Leaves* mostly with more or less parallel sides and mostly acute, only in a few cases acuminate; upper midrib a blunt ridge at least 0.3 mm wide, broader but less prominent below; usually three vascular resin canals, sometimes more. *Buds for pollen cones* mostly 2–3 mm long, either sessile or on a short peduncle, the secondary pollen cone buds when they first appear a round ball of overlapping imbricate scales. *Pollen cones* mostly solitary or in groups of no more than 3. Apex of the microsporophyll a small triangular spur *c.* 0.3–0.5 mm long over a base *c.* 1 mm wide. Foliola of the *female structure* mostly *c.* 2 mm long. *Receptacle* normally formed of two bracts, one of which is fertile and longer than the other or both fertile and equal, the fertile bracts 8–10(–12) mm long before becoming fleshy, in most species the ripe receptacle is known to be red. *Seed* with its covering 7–12 mm long by 5–8 mm diam., in most species more particularly 9–10 mm long and 6–7 mm diam., globular, apex mostly blunt. Peduncle mostly 5–10(–15) mm long but shorter in some species.

Distr. From Nepal throughout *Malesia* to the Solomon Islands, Fiji and Tonga 10 *spp.* The range is greatly dominated by the impressive, wide distribution of *P. neriifolius*, the most widespread species of the genus, which covers virtually the entire Asian–Pacific wet tropical forest zone. The one highland species, *P. rubens*, is also widely distributed, otherwise the species are more local but combine to form a nearly continuous slightly overlapping series from Sumatra to Tonga. All but 2 *spp.* lie within Malesia.

Ecol. Scattered either in primary rain-forest (but rarely encountered in the dipterocarp forest: *P. neriifolius*), generally prominent in ridgetop mossy forests at moderate elevations (most species), or widespread in mountain forests at higher elevations (*P. rubens*). One species is confined to riverbanks.

Note. *Sect. Foliolatus* consists of a group of closely related species which lack the specialized characteristics which distinguish each of the remaining sections of the genus.

KEY TO THE SPECIES

1. Midrib on the upper side of the leaf prominent, at least 0.3 mm high and less than 1 mm wide (primary budscales no more than 5 mm long).
2. Juvenile leaves acuminate, midrib bold with vertical sides. Primary budscales 1–1.5 mm wide.
3. Leaf at least 7 cm by 10 mm, not apiculate, new leaves green to reddish, midrib 0.4–0.8 mm wide (where only 0.4–0.5 mm wide the leaf usually acuminate). Pollen cones normally sessile. Ripe receptacle red. **1. P. neriifolius**
3. Adult leaf no more than 6 cm by 10 mm, often apiculate, new leaves bright red, midrib 0.3 mm wide. Pollen cones often on a short peduncle. Ripe receptacle often purple .... **2. P. rubens**
2. Juvenile leaves never acuminate, midrib with sloping sides. Primary budscales 2 mm wide (pollen cones usually pedunculate).
4. Leaf at least 7 cm by 10 mm, linear-oblong (midrib 0.5 mm wide). Pollen cone usually solitary. Receptacle often with three fleshy bracts .... **3. P. archboldii**
4. Adult leaf no more than 9 cm by 9 mm, elliptic. Pollen cones usually in clusters of 2–3. Receptacle of two bracts only .... **4. P. insularis**

1. Midrib on the upper side of the leaf at least 1 mm wide or indistinctly raised or both.
5. Midrib prominently raised above, 0.3 mm high, often drying to a channel below (leaves distinctly thicker than usual for the genus). Primary budscales may reach at least 1 cm long.
6. Leaves more than 10 cm long. Female peduncle 9–15 mm. Primary budscales and leaves deflexed **5. P. deflexus**
6. Leaves less than 10 cm long. Female peduncle 2 mm. Primary budscales and leaves erect **6. P. borneensis**
5. Upper surface of leaf flat or nearly so, lower surface generally lacking a channel (leaves not thicker than usual for the genus). Budscales never as long as 1 cm.
7. Leaves lanceolate or narrowly linear . . . . **7. P. levis**
7. Leaves oblong, not tapering . . . . **8. P. spathoides**

1. Podocarpus neriifolius D.DON in Lambert, Gen. Pinus ed. 1 (1824) 21; Prod. Fl. Nep. (1825) 55; SPRENG. Syst. Veg. 3 (1826) 889; BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 40; ENDL. Syn. Conif. (1847) 215; PARL. Bot. Mag. 78 (1852) t. 4655; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 381; PARL. in DC. Prod. 16, 2 (1868) 514; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 104; HOOK.*f.* Fl. Br. Ind. 5 (1888) 649; STAPF, Trans. Linn. Soc. II, Bot. 4 (1894) 249; WARB. Monsunia 1 (1900) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 80; K. & V. Bijdr. 10 (1904) 265; MERR. Philip. J. Sc. 1 (1906) Suppl. 24; FOXW. Philip. J. Sc. 2 (1907) Bot. 258; GIBBS, J. Linn. Soc. 39 (1909) 183; FOXW. Philip. J. Sc. 6 (1911) Bot. 162; RIDLEY, J. Str. Br. R. As. Soc. *n.* 60 (1911) 57; KOORD. Exk. Fl. Java 1 (1911) 65, f. 3; GIBBS, Ann. Bot. 26 (1912) 549, t. 51, f. 48–51, t. 53, f. 78; KOORD. Atlas 2 (1915) t. 589; Fl. Tjibodas 1 (1922) 3; RIDLEY, Fl. Mal. Pen. 5 (1925) 281; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 247; HICKEL, Fl. Gén. I.-C. 5 (1931) 1069; WASSCHER, Blumea 4 (1941) 437, *incl. var. polyantha* WASSCHER, *l.c.* 455; GRAY, J. Arn. Arb. 39 (1958) 460, 467; BACKER & BAKH.*f.* Fl. Java 1 (1963) 90; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 187, f. 805; DE LAUB. Kalikasan 7 (1978) 139. — *Nageia neriifolia* (D.DON) O.K. Rev. Gen. Pl. 2 (1891) 800. — *P. neglecta* BLUME, Rumphia 3 (1849) 213; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 396; DE BOER, Conif. Arch. Ind. (1866) 21, t. II, 2; PARL. in DC. Prod. 16, 2 (1868) 516; WARB. Monsuna 1 (1900) 193. — *Nageia neglecta* (BLUME) O.K. Rev. Gen. Pl. 2 (1891) 800. — *P. discolor* BLUME, Rumphia 3 (1847) 213; MIQ. Fl. Ind. Bat. 2 (1859) 1074; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 396; DE BOER, Conif. Arch. Ind. (1866) 23, t. III, 1; PARL. in DC. Prod. 16, 2 (1868) 518; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 104; WARB. Monsunia 1 (1900) 193. — *Nageia discolor* (BLUME) O.K. Rev. Gen. Pl. 2 (1891) 800. — *P. leptostachya* BLUME, Rumphia 3 (1849) 214; MIQ. Fl. Ind. Bat. 2 (1859) 1073; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 392; DE BOER, Conif. Arch. Ind. (1866) 19, t. II, 1; PARL. in DC. Prod. 16, 2 (1868) 515; WARB. Monsunia 1 (1900) 193. — *Nageia leptostachya* (BLUME) O.K. Rev. Gen. Pl. 2 (1891) 800. — *P. junghuhniana* MIQ. Pl. Jungh. 1 (1851) 2; Fl. Ind. Bat. 2 (1859) 1073. — *P. polyantha* (WASSCHER) GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 191, f. 811. — *P. decipiens* GRAY, J. Arn. Arb. 36 (1955) 204; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 225, f. 844.

Tree (3–)5–30(–45) m tall, 10–100 cm diam., clear bole up to 20 m; crown often dome-shaped. Foliage buds 2–5 mm long, occasionally longer, the primary scales often spreading. *Juvenile leaves* 15–24 by up to 2.4 cm, acuminate and acute, narrowing abruptly at the base to a short petiole, becoming linear-lanceolate and *c.* 1.6 cm wide on older fast-growing saplings in open forest situations. *Leaves of mature trees* similar with a short petiole up to 6 mm. Shade leaves acuminate, 8–12 by 1.2–1.8 cm. More exposed leaves linear-lanceolate, 12–18 by 1.1–1.5 cm or on particularly large trees more nearly linear and 7–10 by 1–1.1 cm. Midrib abruptly raised on the upper side of the leaf at least 0.3 mm high and usually 0.6–0.8 mm wide but as little as 0.4 mm wide on less vigorous leaves or in the Borneo region on most leaves. *Pollen cones* solitary or in groups of two or most commonly three, sessile. *Receptacle* bright red when mature.

Distr. From Nepal, Sikkim, Assam (Khasya), Thailand and Indochina through Malesia to the Solomon and Fiji Islands; in *Malesia*: Malaya, Sumatra (incl. Simalur I.), throughout Java and Borneo (incl. Karimata I.), the Philippines (Mindanao), Celebes, the Lesser Sunda Islands (Bali, Flores), the Moluccas (Obi, Ceram, Halmaheira), and New Guinea (incl. New Britain, New Ireland, Rossel I.,

Fig. 45. Range of *Podocarpus neriifolius* D.DON.

Manus I., Biak, Job I., and Numfoor), common in many islands. Fig. 45.

Ecol. Scattered and locally common in primary rain-forests from near sea-level to *c.* 2100 m. In most areas it appears as an understory tree with occasional much larger, emergent specimens in the canopy but in other areas, such as Java, Fiji, *etc.* it is normally a canopy tree.

Habitats vary: rarely riverine, often on rocky hilltops, in mossy forest, twice recorded from limestone, and twice from swampy forest. Also as to soils there is diversity: in Sarawak it is found on kerangas in heath forest and on sandstone ridges, but also on andesitic laterites, which is the common latosol in Java, and sandy clay. In the Morobe District (New Guinea) it is recorded from ultrabasic.

As to associates it is recorded from pelawan (*Tristania*) forest on sandstone ridges in S. Borneo; in the Javanese mountain forest its codominants are *Dacrycarpus imbricatus* and *Altingia noronhae*; in New Britain it occurs in the hills with *Pometia* and *Calophyllum*, in the montane forest in New Ireland with *Fagaceae*, *Eugenia* and *Schizomeria*; in the Morobe District (New Guinea) it is associated with *Anisoptera* and *Flindersia* in the canopy.

Field notes. The bole is columnar, as usual; very rarely buttresses were recorded on field labels, 120 by 60 cm and 200 by 40 cm; sometimes the base was slightly spurred.

Uses. A valuable timber tree, used for construction.

Vern. *Brown pine*, E; Malaya: *jati bukit*, Pahang; Sumatra: *ambai ayam*, Indragiri, *hatang*, Tapanuli, *kayu tadji*, Palembang, *minangkas*, Bencoolen, *naru dotan*, Simalur I., *sito bu hotang*, Karo-Batak; Java: *antoh*, J, Japara, *ki bima, ki merak, ki pantjar, ki putri*, S; Borneo: *belah buloh*, Lawas, Sarawak, *djadjaruman*, Sampit, *ki beling*, Sabah; Celebes: *kurniah*, Nokilalaki; Lesser Sunda Islands: *hadjo ketong, hadju pinis rona*, Flores; Moluccas: *bitaö*, Halmaheira; West New Guinea: *aiwimunuwamee*, Biak lang., *bung*, Mayu lang., *buskagidji, butsgagyi*, Andai, Manikiong lang., *gedorra*, Fakfak, Esania lang., *kayu tjina merah*, Kp. Baros, *korrikain*, Tehid lang., *uwa*, Amberbaken lang., *wajar*, Mandobo lang., *wasabraren*, Numfoor I.; East New Guinea: *isimberi*, Nindewari, *sipiri*, Kikori R., *sirau*, Bulolo, Gairana dial.

Notes. Much the most widespread species of the genus, but other species are very commonly identified under this name causing confusion as to its exact character and retarding the recognition of the other species.

In spite of the great geographic range, only slight variation exists within the species. The most distinct element is in the substantially isolated occurrence in Fiji where primary foliage budscales can reach 5 mm and where extra vascular resin canals are often found in the leaves (*P. decipiens*). In Borneo the midrib on the upper surface of the leaf is weak while from India to southeastern Asia the leaves are more commonly lanceolate and the foliage buds are usually no more than 2 mm long with barely spreading primary scales.

2. Podocarpus rubens DE LAUB. Blumea 30 (1985) 266. — *P. neriifolius var. timorensis* WASSCHER, Blumea 4 (1941) 451. — *P. pilgeri* (*non* FOXW.) VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 29, f. 39A. — **Fig. 46.**

Fig. 46. *Podocarpus rubens* DE LAUB. Twig with seed-bearing structure showing two fruits on their receptacles (after NGF 6980).

Tree 2–30 m tall, 4–36 cm diam. Foliage buds 2–3 mm long, the primary scales erect or slightly spreading. Developing leaves bright red. *Juvenile leaves* linear, narrowly acuminate, becoming apiculate, 6–8 by 1.1–1.4 cm, narrowing at the base to a 2–3 mm petiole. *Adult leaves* linear to elliptic, 3–6 by 0.6–1 cm, apex acute to rounded and often apiculate, base same as juvenile leaves, margin revolute, midrib above 0.3 mm high with vertical sides, 0.3 mm wide. *Pollen cones* solitary or in threes, sessile or on a short peduncle. *Receptacle* becoming first red then purple.

Distr. *Malesia*: Central to S. Sumatra, Celebes (Central: Latimodjong & Kambuno Mts; SW: G. Bonthain), Lesser Sunda Islands (Timor: G. Mutis), and New Guinea (incl. Normanby & New Britain). Fig. 47.

Ecol. Scattered as a medium-sized, substage tree in primary rain-forest mostly above 1500 m but as

Fig. 47. Range of *Podocarpus rubens* DE LAUB.

low as 800 m on smaller islands or locally common to dominant as a small tree on ridges between 2000 and 3000 m or occasionally higher. Mostly on latosols, in New Guinea in Fagaceous mossy forest, rarely in swampy forest on peaty soils with *Dacrydium*.

Vern. West New Guinea: *bebi-è*, Wissel Lakes, Kapauko lang., *ungpop*, Arfak, Hattam lang.; East New Guinea: *bin*, Ingembit village, W. Distr., *kaip*, Wabag, Enga lang., *nelil*, Mt Tangis, New Britain, *sukou*, Wigote, Wapi lang.

Notes. The bright red colour of a new flush of leaves which has been seen in this species can make the trees quite conspicuous. Herbarium specimens can resemble *P. pilgeri* but the upper midrib of the leaf rises *c.* 0.3 mm with vertical sides, while that of *P. pilgeri* is hardly 0.2 mm high with sloping sides. Leaves of *P. pilgeri* which approach *P. rubens* in size are from shady situations and are distinctly thin and delicate while those whose texture resembles the coarse rigid leaves of *P. rubens* are no more than 4–6 mm wide. The always solitary pollen cone of *P. pilgeri* is distinctly more slender and the ripe receptacle is red. Unique in the section is that most specimens of *P. rubens* have some leaves with a narrow-acuminate or more or less apiculate apex.

The specimens of *P. rubens* from Ambon have a continuous upper hypoderm while elsewhere there are only scattered upper hypoderm cells and vascular sclereids.

Specimens assigned to *P. rubens* from Normanby I. and New Britain have quite blunt leaves with a less prominent midrib. In all other ways they conform to the species but it is possible that they represent a different taxon.

The specimen ICHLAS 166 from a high elevation in Sumatra seems too long and narrow to be placed comfortably here, even though more typical specimens exist nearby at lower elevation. The foliage bud is rather robust and the lateral resin canals are quite large. It resembles *P. brevifolius* and *P. crassigemmis* and could represent a new allied species.

3. Podocarpus archboldii N.E.GRAY, J. Arn. Arb. 39 (1958) 452; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 177; DE LAUB. Blumea 26 (1980) 140.

Tree 10–40 m tall, 30–100 cm diam., clear bole up to 12–24 m, sometimes slightly fluted. Foliage buds 2–4 mm long, the primary scales slightly spreading. *Juvenile leaves* to at least 18 by 1.6 cm, otherwise like adult leaves. *Adult leaves* linear to linear-lanceolate, 7–12 by 1–1.4 cm, apex broadly acute, base abruptly narrowed to a petiole up to 5 mm long, midrib above blunt, 0.3 mm high, with sloping sides, 0.5 mm wide. *Pollen cones* solitary, sessile or on a peduncle to at least 4 mm. *Receptacle* often with a third lateral bract smaller than the second bract, red when mature.

Distr. *Malesia*: New Guinea. Fig. 48.

Ecol. Scattered and locally common in the canopy of mixed mid-mountain rain-forest with *Castanopsis* from 720 to 2200 m.

Vern. West New Guinea: *mu, soa*, Kebar lang.; East: *sarau*, Bulolo, Geraina.

Note. Sterile specimens strongly resemble *P. neriifolius* but strictly lack acuminate leaf tips and the upper midrib has sloping, not vertical sides. Unlike *P. neriifolius* the pollen cones are sometimes pedunculate and the fruit receptacle sometimes has an extra lateral bract.

4. Podocarpus insularis DE LAUB. Blumea 30 (1985) 266.

Small to medium-sized tree, 3–39 m tall, up to 20–60 cm diam., bole up to 24 m. Foliage buds 2.5–3 mm long and up to 3.5 mm diam., the primary budscales strongly spreading. *Juvenile leaves* linear, to 15 by 1.4 cm. *Adult leaves* elliptic, 5.5–9 cm by 7–9 mm, apex acute, narrowed at the base to a 3–4 mm petiole; midrib above 0.3 mm high with vertical sides, 0.3 mm wide. *Pollen cones* solitary or in threes, sessile or with a short peduncle. *Receptacle* red when mature.

Distr. New Hebrides and all Solomon Islands; in *Malesia*: New Guinea and adjacent islands: Rossel, Sudest, Misima, Woodlark, Fergusson, and New Britain. Fig. 49.

Ecol. A good-sized lesser canopy tree, scattered and locally common in wet rain-forest, also in *Nothofagus* forest with undergrowth of *Nastus*, from near sea-level to 1680 m, and smaller trees from low ridge habitats.

Vern. East New Guinea: *dala, tunum*, Milne Bay, Daga lang., *ida-ayebo*, Kutubu lang.

Note. This species is distinguished by its rather small and narrow elliptic leaves with narrow but prominent midrib with nearly vertical slides and by the robust compact foliage buds with outward curling scales. Dried specimens sometimes develop a rich red-brown colour on the underside.

5. Podocarpus deflexus RIDLEY, Fl. Mal. Pen. 5 (1925) 283; WASSCHER, Blumea 4 (1941) 427; GRAY, J. Arn. Arb. 39 (1958) 450; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 175, t. 802.

Small tree, 5–10 m tall, to 10 cm diam. Foliage buds *c.* 3 mm long but with the primary budscales up to 12 mm long and curling sharply outward with bluntly rounded apices, the secondary scales much shorter, broader, and rounded. *Juvenile leaves* up to 26 by 1.2–1.5 cm. *Adult leaves* linear to linear-lanceolate, 11–22 cm by 8–10(–13) mm, acute or slightly rounded at the apex, narrowing gradually more or less to a petiole, cuticle thick, often with five vascular resin canals, sharply bent at the base so as to hang downward, midrib above 0.4 mm high and 1 mm broad with indistinct margins, midrib beneath drying to a channel below. *Pollen cones* in groups of three, sessile or with a 2 mm peduncle. Primary pollen cone budscales 2 mm wide. *Receptacle* formed by two fertile bracts and a third shorter sterile bract crowded more or less to one side between the other two. *Seed* 11–12 by 6–8 mm.

Distr. *Malesia*: N. Sumatra (Gajo Lands: G. Ketambe) and Malaya (G. Tahan). Fig. 48.

Fig. 48. Range of *Podocarpus archboldii* N.E.GRAY (A), *P. deflexus* RIDLEY (D), and *P. borneensis* DE LAUB. (B).

Ecol. Rising above and locally dominant in dwarf mountain scrub, 1500–2100 m.

Note. A rather distinctive species, its large smooth leaves and large fruit resembling among others *P. rumphii* and *P. solomoniensis* in other sections of the genus but differing in the key characters of those sections. This species, unlike most of the genus, appears to be monoecious inasmuch as a random field inspection of about a dozen trees showed every single one to bear male buds (fruiting specimens have been collected at a different time of year).

6. Podocarpus borneensis DE LAUB. Blumea 30 (1985) 266. — *P. polystachus var. rigidus* WASSCHER, Blumea 4 (1941) 460; GRAY, J. Arn. Arb. 39 (1958) 471.

Small to medium-sized tree, (2–)5–12(–23) m tall, 2.5–21 cm diam. Foliage buds 4–10 mm long, the primary scales erect. *Juvenile leaves* linear, to 16 by 1.4 cm. *Adult leaves* linear to ovate, (2.5–)4–7.5 (–9) cm by 8–13 mm, narrowing at the base to a 3–5 mm petiole, more or less acute but usually slightly rounded at the apex, thick, with abundant auxillary sclereids, midrib above prominent, 1 mm wide and 0.3 mm high, often drying to a channel below, often crowded around the foliage bud. *Pollen cones* solitary or in threes, sessile or on a short peduncle. *Seed-bearing structure* on a 2 mm peduncle, *receptacle* red when mature. *Seed* with a small crest.

Distr. *Malesia*: Borneo (incl. Karimata Is.). Fig. 48.

Ecol. Locally common or even dominant (Merurong Plateau) on mossy rocky ridges, or scattered in nearby forest, in high kerangas forest and on white, sandy soils, 700–2070 m, one collection from a swamp at 360 m.

Vern. *Bisit*, Sarawak, Kenya lang., *bubung*, Iban lang., *buloh*, Merurong Plateau.

Note. As in *P. deflexus* the leaves are thicker than usual for the genus and the lower midrib dries to a channel. The abundant foliar sclereids is a character shared apparently with *P. novaecaledoniae* in this section.

7. Podocarpus levis DE LAUB. Blumea 24 (1978) 496.

Tree, 8–25(–35) m tall, 16–40 cm diam. Foliage buds 3–9 mm long, the primary scales spreading. *Juvenile leaves* up to 20 by 1.5 cm, narrowly acute. *Adult leaves* linear-lanceolate, 8–14 by 1–1.4 cm, acute or narrowly rounded at the apex, narrowing at the base to a 4–9 mm petiole, stiff, upper hypodermal fibres in a continuous layer, upper midrib a low blunt ridge 0.3–0.5 mm wide and 0.1–0.2 mm high which furthermore often collapses upon drying so that the leaf appears smooth or even channeled, often with five vascular resin canals. *Pollen cones* typical of the section or longer, up to 8 cm long, solitary or in groups of up to three. *Receptacle* often with two bracts fertile and then sometimes with a third shorter sterile bract on one side between the other two, red when mature; foliola 2–4 mm long. *Seed* with its covering 12–13 by *c.* 8 mm.

Distr. *Malesia*: E. Borneo (once; Berau), Celebes, Moluccas (Talaud Is.: Karakelong, Mt Piapi; Ambon: Mt Salhutu & Mt Hori), and West New Guinea (Meos Noom & Japan Is.). Fig. 49.

Ecol. Scattered and locally common in primary rain-forest, from sea-level to 1650 m. In E. Borneo on limestone.

Fig. 49. Range of *Podocarpus insularis* DE LAUB. (east of line) and *P. levis* DE LAUB. (west of line).

Vern. Celebes: *marisa*, Donggala, *sanru*, Malili; New Guinea: *kayu tjina*, Meos Noom, *wasiwarare*, Japen I.

8. Podocarpus spathoides DE LAUB. Blumea 30 (1985) 267.

Tree, 3–20 m tall, to 30 cm diam. Foliage buds 2–6 mm long, the primary scales spreading. *Juvenile leaves* up to 23 mm wide. *Adult leaves* linear, 5–13 by 0.8–2 cm, apex acute or rounded, narrowing abruptly at the base to a 3–5 mm petiole, midrib above broad and obtuse. *Pollen cones* in threes on a short peduncle.

Distr. Solomon Islands; in *Malesia*: E. New Guinea (Louisiades: Rossel I.), N. Moluccas (Morotai: G. Pare), and Malaya (G. Ledang = Mt Ophir; type), all isolated occurrences. Fig. 50.

Fig. 50. Range of *Podocarpus spathoides* DE LAUB.

Ecol. Scattered and locally common at 1000–1200 m in the western two stands and near sea-level in the east.

Note. In Malaya and Rossel I. the foliage buds are no more than 3 mm long, the others are twice as long. In Malaya the trees grow in a summit scrub and are only 3–4 m high, elsewhere collectors report 12–20 m high trees. Perhaps intermediates exist or alternatively more than one similar taxon may be involved here.

2. Section Acuminatus

DE LAUB. Blumea 30 (1985) 267.

Primary foliage buds of variable diameters, at least 4 mm long, often much longer; primary scales erect, lanceolate, with free tips, as long as the bud itself, up to 3 mm wide at the base in vigorous buds but *c.* 1.5 mm wide in weaker buds; secondary budscales acuminate, the secondary bud when it first appears a loose cluster of free scales whose tips resemble the surrounding primary scales. *Leaves* with parallel margins, distinctly acuminate, narrowing more or less abruptly at the base, midrib above at least 0.5 mm wide and 0.3 mm high, broader and less prominent beneath, usually three vascular resin canals, occasionally more. *Buds for pollen cones c.* 3–5 mm long, either sessile or on a short peduncle, secondary scales acuminate, the secondary pollen cone bud when it first appears is briefly a round ball of overlapping imbricate scales. *Pollen cones* 3–5 cm long or longer, occasionally solitary but mostly in groups of three. Apex of the microsporophyll a triangular spur 0.5–0.7 mm long over a broader base. Peduncle of seed-bearing structure variable. *Receptacle* of the seed formed of one or two fertile bracts of variable sizes and one shorter sterile bract, the ripe receptacle red. *Seed* with its covering of variable size, globular, apex blunt or a slight crest.

Distr. From Borneo to Queensland 3 *spp.*, of which 2 in *Malesia*: in Borneo and New Guinea respectively.

Ecol. Low elevation primary rain-forest understory trees, in one case also common along disturbed forest margins.

Note. The only section with both acuminate secondary budscales and acuminate leaves.

KEY TO THE SPECIES

1. Seed and its covering at least 11 by 8 cm, not crested. Adult leaves mostly more than 17 mm wide. Female peduncle at least 4 mm long. Plant lacking rhizomes .... **9. P. ledermannii**
1. Seed and its covering less than 11 by 8 mm, slightly crested. Adult leaves less than 17 mm wide. Female peduncle *c.* 1 mm long. Plant with rhizomes .... **10. P. micropedunculatus**

9. Podocarpus ledermannii PILGER, Bot. Jahrb. 54 (1916) 210; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; WASSCHER, Blumea 4 (1941) 456; N.E.GRAY, J. Arn. Arb. 39 (1958) 447; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 173, t. 827; DE LAUB. Blumea 26 (1980) 140. — *P. idenburgensis* N.E.GRAY, J. Arn. Arb. 39 (1958) 447; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 171, t. 826. — *P. ridleyi* N.E.GRAY, J. Arn. Arb. 39 (1958) 426, f. 1.

Tree, 4–26(–33) m tall, 8–60 cm diam. Foliage buds 4–8 mm long by 3–4 mm in diam., the primary budscales more or less spreading. *Juvenile* and *adult shade leaves* linear, 11–22 by 2–2.4 cm, narrowing abruptly to an acuminate apex and at the base to a 4–10 mm petiole; *leaves more exposed* to the sun no more than 16–18 mm wide, weakly acuminate if at all and narrowing less abruptly at the base; midrib above broad and rounded, 1.5–2 mm wide and *c.* 0.6 mm high, sometimes collapsing on dried specimens to a small narrow ridge. *Pollen cones c.* 4.5 cm long, grouped on a 3–4 mm peduncle. *Seed-bearing structure* on a 4–15 mm peduncle; foliola 2 mm long; receptacle 9–16 mm long. *Seed* with its covering 11–13 by 9–10 mm, slightly crested.

Distr. *Malesia*: New Guinea and New Britain. Fig. 51.

Ecol. Scattered and locally common in primary rain-forest understory from low elevation to at least 1800 m.

Vern. West New Guinea: *sua*, Kebar, *bèbieai*, Kapauko lang.; East New Guinea: *babako*, Aijura, Anona; New Britain: *neleel*, Cape Gloucester, *nelil*, Mt Talawe.

Note. Leaves in the type collection are at the short and broad extremes for the species. Leaves in two examples were found to have two large additional vascular resin canals and one of these also had a continuous upper hypoderm.

10. Podocarpus micropedunculatus DE LAUB. Blumea 30 (1985) 268.

Shrub or small tree, 1–7(–13) m tall, 5–20 cm diam., with rhizomes which spread under the forest litter. Foliage buds 6–15 mm long by 1.5–3 mm diam. *Juvenile leaves* 14–18 by 1.5–2.1 cm. *Adult leaves* 8–17 by 1–1.5 cm; petiole 3–5 mm; midrib above 0.5–0.8 mm wide and 0.4 mm high, drying to a channel below. *Pollen cones* 3.5–7.5 cm, sessile or with a short peduncle. Primary pollen cone budscales 4–5 mm long. *Seed-bearing structure* on a 1 mm peduncle; foliola 3–4 mm; receptacle 8–10 mm long. *Seed* with its covering 8–10 by 6 mm with a small crest.

Distr. *Malesia*: Borneo (Sarawak: Marudi For. Res.; Brunei; Sabah: Papar, Tawao). Fig. 51.

Fig. 51. Range of *Podocarpus ledermannii* PILGER (L) and *P. micropedunculatus* DE LAUB. (M).

Ecol. Scattered in understory of *Agathis* forest or forming a major element in thickets along the margins of clearings, mostly on sandy, podzolic soils, kerangas, sandstone, humic peaty podsols of raised beaches, and peat-swamp forest, from sea-level to occasionally as much as 500 m. Sometimes associated with *Dryobalanops rappa* or *Shorea albida*.

Vern. Sarawak: *kayu china*; Sabah: *kayu tjina*.

Note. Propagation by rhizomes is a remarkable character otherwise unknown among erect conifers and obviously facilitates rapid appropriation of disturbed situations.

3. Section Globulus

DE LAUB. Blumea 30 (1985) 268.

Primary foliage bud a globular head of completely imbricate scales, gradually expanding with the growth of a new shoot until the secondary bud, also globular, erupts; primary budscales acute to more or less rounded, *c.* 1.5–2 mm long; secondary scales oval and blunt. *Leaves* with parallel sides or somewhat lanceolate, slightly rounded at a narrow apex to broadly rounded and sometimes acuminate, midrib above blunt, 0.2 mm high and at least 0.5 mm broad, broader and indistinct below, 3 vascular resin canals. *Buds for pollen cones* sessile or on a short peduncle, the primary scales *c.* 1.5 mm long; the secondary pollen cone bud similar to the secondary foliage bud. *Pollen cones* mostly 2.5–4.5 cm long (smaller in some species), solitary or in groups of three. Apex of the microsporophyll mostly a small triangle less than 0.5 mm long (longer in *P. nakaii*). *Seed-bearing structure* on a peduncle of variable length; *receptacle* formed of two bracts, one of which is longer and mostly 7–9 mm long (longer in *P. lucienii*) or both are fertile and equal, where known the ripe receptacle red. *Seed* with its covering 8–10 mm long by 5.5–6 mm diam. (or larger in some species), globular, apex blunt or in some species with crest.

Distr. From Vietnam and Formosa to Borneo and New Caledonia 6 *spp.*; in *Malesia*: 2 *spp.*, in Sumatra/Malaya and Borneo respectively.

Ecol. Mostly short trees of low (to 2000 m) elevation tropical forest either in the understory of primary or secondary rain-forest (occasionally larger and in the canopy), on exposed mossy ridges, or in short open forest.

Note. The gap between Borneo and New Caledonia is largely filled by the related *sect. Rumphius* which overlaps this section geographically only slightly. The primary budscales in *sect. Rumphius* rather than being completely imbricate and overlapping more or less meet at their apices with usually one or more actually curling outward at their apex while, in addition, the pollen cones in *sect. Rumphius* are normally in clusters of more than three and all the species of *sect. Rumphius* occur as large canopy trees.

KEY TO THE SPECIES

1. Seed and its covering with a small crest; foliola 2 mm long. Adult leaves not acuminate, 9–15 mm wide **11. P. globulus**
1. Seed and its covering without a crest; foliola less than 1 mm long. Adult leaves distinctly acuminate, 14–21 mm wide .... **12. P. teysmannii**

11. Podocarpus globulus DE LAUB. Blumea 30 (1985) 269.

Tree, 3.5–27 m tall, to 18 and more cm diam. *Juvenile leaves* 7.5–16 by 1.5–2.4 cm, abruptly acuminate. *Adult leaves* linear, narrowing more or less abruptly at the base to a 2–3 mm petiole, acute to rounded apex, 3.5–8 by 0.9–1.5 cm, midrib above 0.5–0.7 mm wide. *Pollen cones* 2.5–4.5 cm, solitary or occasionally in threes, sessile or on a short (1 mm) peduncle. *Seed-bearing structure* on a 3–4 mm peduncle; foliola 2 mm and early deciduous. *Seed* with its covering with a brief crest.

Distr. *Malesia*: northern part of Borneo (Sarawak; Sabah: Mt Silam). Fig. 52.

Ecol. In primary rain-forest or mossy forest on ridges and peaks from 300 to 1500 m apparently where the forest is not dominated by dipterocarps. In some cases at least, an ultrabasic soil is indicated.

Vern. *Sapiro*, Lawas, Murut lang.

Fig. 52. Range of *Podocarpus globulus* DE LAUB. (G) and *P. teysmannii* MIQ. (T).

12. Podocarpus teysmannii MIQ. Fl. Ind. Bat. 2 (1859) 1072; DE BOER, Conif. Arch. Ind. (1866) 14, t. 1; PARL. in DC. Prod. 16, 2 (1868) 516; WARB. Monsunia 1 (1900) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 81. — *Nageia teysmannii* (MIQ.) O. K. Rev. Gen. Pl. 2 (1891) 800. — *P. neriifolius var. teysmannii* (MIQ.) WASSCHER, Blumea 4 (1941) 453; N.E.GRAY, J. Arn. Arb. 39 (1958) 468; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 189.

Tree, 4–12 m tall, up to 30 cm diam. *Juvenile leaves* to 16 by 2.7 cm. *Adult leaves* linear, 9–13 by 1.4–2.1 cm, acuminate, narrowing more or less abruptly at the base to 4–7 mm petiole, midrib above 0.6–0.8 mm wide. *Pollen cones* 2.5 cm, solitary or occasionally paired, sessile. *Seed-bearing structure* on a 6–11 mm peduncle; foliola 1 mm and early deciduous.

Distr. *Malesia*: Malaya and Sumatra (Westcoast Res.), incl. Riouw-Lingga and Banka Is. Fig. 52.

Ecol. Understory tree of primary or secondary rain-forest from sea-level to occasionally as high as 1140 m, in Banka on granite sand.

Vern. Sumatra: *kalek rotan*, Westcoast.

4. Section Longifoliolatus

DE LAUB. Blumea 30 (1985) 269.

Primary foliage budscales erect, narrowly lanceolate with free tips, occasionally as little as 4 mm long on weak shoots but mostly at least 6 mm long and often much longer; secondary budscales acuminate, the secondary bud when it first becomes visible a cluster of erect scale tips shorter than the primary scales. *Leaves* either linear and no more than 11 mm wide or narrowly lanceolate, narrowing gradually at the base, midrib above variable in width and mostly *c.* 0.3 mm high but lower in some species, broader and less prominent beneath (and in some species drying into a channel), in most species more than 3 vascular resin canals, frequently a well-developed or continuous upper hypoderm, especially where there are no extra resin canals. *Buds for pollen cones* 3–4 mm long, mostly sessile but with a short peduncle in a few species, the primary scales mostly 1.5 mm wide at the base, occasionally wider; secondary scales mostly acuminate, the secondary pollen cone bud when it first appears sometimes still a ball of overlapping scales but more often with the scale tips starting to separate. *Pollen cones* variable in length, slightly greater in diameter than usual for the genus where the apex of the microsporophyll is longer than usual, solitary or sporadically in groups of 2 or 3. Apex of the microsporophyll usually a spur *c.* 0.5 mm long on a wider base but longer in some species and shorter in others. *Seed-bearing structure* on a peduncle (2–)7–15(–20) mm long; foliola in all species to over 3 mm and only sometimes as little as 2 mm in any species. *Receptacle* formed of at least two bracts at least one of which is fertile and longer, while often, or in some species usually, two are equal, with one to three smaller bracts crowded between them and sometimes one or two of these smaller bracts fertile, the larger bracts variable in size between the species but at least 9 mm long; where known the ripe receptacles are red to dark red. *Seed* with its covering also variable in size, at least 8 mm long by 6 mm diam., globular, in some species with a weak crest.

Distr. Mostly in highly localized stands from Sumatra to Fiji, 10 *spp.*, 5 of which are in *Malesia*.

Ecol. Mostly small or stunted trees (or even decumbent) in more or less specialized habitats, particularly over ultrabasic soils.

Notes. This section can be divided roughly into two parts, one with more or less parallel-margined leaves with extra resin canals and normally at least two fruits on each fertile structure as well as small pollen cones 10–28 mm long and a strong relationship to ultrabasic soils; the other part with lanceolate leaves, which only in some cases have extra resin canals and normally only one fruit in each fertile structure as well as larger pollen cones 3–4.5(–6) cm long and a relationship to a variety of habitats. In all species the foliage buds on vigorous shoots surpass 8 mm, a condition found in the subgenus only elsewhere in *sect. Acuminatus*. The female foliola usually or always at least 3 mm long are rare elsewhere in the genus.

KEY TO THE SPECIES

1. Pollen cones less than 3 cm long; leaf elliptic, somewhat revolute, adult leaves less than 5 cm long **13. P. gibbsii**
1. Pollen cones more than 3 cm long; leaf mostly lanceolate or linear-lanceolate, not revolute, adult leaves at least 5 cm long.
   2. Leaf linear-lanceolate or linear, midrib broad and blunt on the upper side (no crest on fruit) **14. P. confertus**
   2. Leaf lanceolate, midrib sharp and narrow on the upper side.

3. Leaves more than 7 mm wide; scales at base of pollen cone long triangular; fruit with a crest.
    4. Leaves mostly over 10 mm wide; foliola at base of receptacle more than 3 mm long; bud for pollen cone 4–5 mm in diameter; pollen cone initially sessile, when mature with an elongated scaly base **15. P. bracteatus**
    4. Leaves mostly less than 10 mm wide; foliola at base of receptacle up to 3.4 mm long; bud for pollen cone *c.* 2 mm in diameter; pollen cone with a short peduncle to 2 mm .... **16. P. pseudobracteatus**
3. Leaves less than 8 mm wide; scales at base of pollen cone broad and rounded; fruit blunt **17. P. atjehensis**

13. Podocarpus gibbsii N.E.GRAY, J. Arn. Arb. 39 (1958) 429; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 155, t. 803.

Tree 2.5–20 m tall. Foliage buds 4–9 mm long. *Juvenile leaves* linear, acute, 4–9 cm by 5–9 mm. *Adult leaves* linear to ovate, 2–5 cm by 4–7 mm, acute to almost rounded at the apex, narrowed at the base to a 1–3 mm petiole; midrib above weakly developed, 0.5–0.7 mm wide and 0.1–0.2 mm high and often collapsing upon drying leaving a weak depression with a narrow ridge in the centre, upper hypoderm continuous. *Pollen cones* 1–1.5 cm, sessile, solitary or occasionally a pair; apex of microsporophyll triangular, up to 0.8 mm long. *Seed-bearing structure* on a peduncle at least 3 mm long; foliola 4 mm long; receptacle formed of two unequal bracts; mature seed unknown.

Distr. *Malesia*: Borneo (Sabah: Mt Kinabalu). Fig. 53.

Fig. 53. Range of *Podocarpus gibbsii* N.E.GRAY (G) and *P. atjehensis* (WASSCHER) DE LAUB. (A).

Ecol. Mossy ridges between 1200 and 2400 m, mostly or always on ultrabasic soil.

Note. The leaves generally resemble those of *P. pilgeri*, a species which is not otherwise similar at all.

14. Podocarpus confertus DE LAUB. Blumea 30 (1985) 271.

Tree 1–36 m tall. Foliage buds 6–10 mm long. *Juvenile leaves* up to 20 by 1.2 cm. *Adult leaves* linear to linear-lanceolate, 5–12 cm by 7–11 mm, acute, narrowing at the base to a 3–6 mm petiole; midrib above obtuse, 1 mm wide and 0.2–0.3 mm high, collapsing when dry to form a narrow irregular ridge or becoming completely flat, upper hypoderm continuous. *Pollen cones* 3–4.5 cm, sessile, solitary or occasionally in pairs; apex of microsporophyll triangular, 0.3–0.5 mm long. *Seed-bearing structure* on a 5–13 mm peduncle; foliola 5–6 mm long; receptacle 8–12 mm, formed of two unequal bracts. *Seed* with its covering 10–11 by 6–6.5 mm.

Distr. *Malesia*: Borneo (Sabah: Mt Silam). Fig. 54.

Ecol. In dense local populations on various poor soils some or most of which are ultrabasic; subdominant in somewhat open and sometimes stunted forest from 90 to 1200 m.

15. Podocarpus bracteatus BLUME, En. Pl. Jav. 1 (1827) 88; BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 40; ENDL. Syn. Conif. (1847) 216; BLUME, Rumphia 3 (1849) 214, t. 172, f. 1; MIQ. Pl. Jungh. 1 (1851) 2; Fl. Ind. Bat. 2 (1859) 1072; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 391; DE BOER, Conif. Arch. Ind. (1866) 16; PARL. in DC. Prod. 16, 2 (1868) 515; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 104; WARB. Monsunia 1 (1900) 192. — *P. neriifolius var. bracteatus* (BLUME) WASSCHER, Blumea 4 (1941) 449; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 189, t. 806. — *P. bracteatus var. brevipes* BLUME, Rumphia 3 (1849) 214; MIQ. Pl. Jungh. 1 (1851) 2; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 392; PARL. in DC. Prod. 16, 2 (1868) 515. — *P. neriifolius var. brevipes* (BLUME) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 81; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 187. — *P. neriifolius* (*non* D.DON) STEEN. Mt. Fl. Java (1972) t. 13, f. 1.

Tree 10–40 m tall, 15–100 cm diam. Foliage buds 5–12 mm long. *Juvenile leaves* up to 23 by 2 cm. *Adult leaves* distinctly lanceolate, 6–14 cm by 9–14 mm, narrowly acute, narrowing at the base to a 2–4 mm petiole, sometimes with 5 vascular resin canals, midrib above a sharp ridge 0.4 mm wide and 0.3 mm high, sometimes collapsing when dried into a trough. *Pollen cones* 3.5–6 cm by 3–4 mm, sessile but elongating when mature through the scaly base as well as the zone of microsporophylls and the scales then following, the elongated scaly base up to 8 mm long, solitary or occasionally in pairs; apex of microsporophyll *c.* 1 mm long. *Seed-bearing structure* on a 10–20 mm peduncle; foliola 4–5 mm long; receptacle 10–14 mm long, often with two fertile bracts and additional bracts between them. *Seed* with its covering including a small crest, 11–14 by 7 mm.

Distr. *Malesia*: N. & Central Sumatra (rare), throughout Java and the Lesser Sunda Islands (Flores: Mt Ranaka). Fig. 54.

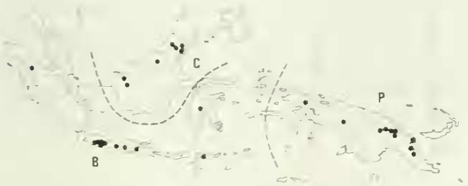

Fig. 54. Range of *Podocarpus confertus* DE LAUB. (C), *P. bracteatus* BLUME (B), and *P. pseudobracteatus* DE LAUB. (P).

Ecol. Scattered in the canopy of moist mountain rain-forest from 1000 to 2600 m or occasionally as low as 400 m.

Uses. An excellent timber tree.

Vern. Sumatra: *kayu unung unung*, Toba Batak; Java: *bima*, J (Pekalongan), *ki marak, ki pantjar, ki putri*, S.

Note. The most common *Podocarpus* of the mountain forests of Java. *Podocarpus neriifolius* also occurs there, but rarely above 1600 m, while *P. bracteatus* is common to over 2000 m. Sterile specimens of the two are sometimes similar, but *P. bracteatus* has a narrower midrib, longer budscales, and a more distinctly lanceolate shape.

16. Podocarpus pseudobracteatus DE LAUB. Blumea 26 (1980) 142. — *P. archboldii var. crassiramosus* N.E.GRAY, J. Arn. Arb. 39 (1958) 453.

Tree 1–15 m tall, 5–20 cm diam. Foliage buds 5–14 mm long. *Juvenile leaves* linear-lanceolate, up to 22 by 1.7 cm. *Adult leaves* linear-lanceolate to lanceolate or exceptionally elliptic, 6–15 cm by 7–12 mm, narrowly acute, tapering more or less abruptly at the base to a 2–4 mm petiole; midrib above a prominent narrow ridge with nearly vertical sides, 0.4–0.5 mm wide and 0.3–0.4 mm high. *Pollen cones* 4–4.5 cm, on a short peduncle up to 2 mm long, solitary; apex of the microsporophyll 0.5–0.7 mm long. *Seed-bearing structure* on a 2–5 mm peduncle; foliola 2.5–3 mm long, often thick and lanceolate; *receptacle* 7–11 mm long, formed of two bracts and becoming first orange, then red, then almost black when ripe. *Seed* with its covering 10–11 by 8–9 mm, blunt.

Distr. *Malesia*: New Guinea. Fig. 54.

Ecol. Scattered and locally common in the understory of mossy *Castanopsis-Nothofagus* forest and *Dacrydium* swamp forest, sometimes entering the alpine shrubbery, from 1740 to 2850 m.

Vern. East New Guinea: *kaip*, Wabag, Enga lang., *kebu*, Tari Gap, *puling*, Togoba, Chimbu.

17. Podocarpus atjehensis (WASSCHER) DE LAUB. Blumea 30 (1985) 271. — *P. neriifolius var. atjehensis* WASSCHER, Blumea 4 (1941) 450; N.E.GRAY, J. Arn. Arb. 39 (1958) 466; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 189.

Tree 8–15 m tall, 20 cm diam. Foliage buds 6–14 mm long. *Adult leaves* linear-lanceolate to lanceolate, 7–11 cm by 6–8 mm, narrowly acute, narrowing somewhat gradually at the base to a 3–4 mm petiole, cuticle thick, sometimes with lateral vascular resin canals distinctly larger than the median canal, midrib above a prominent ridge with nearly vertical sides, 0.2–0.3 mm wide, 0.2 mm high. *Pollen cones* 3.5 cm, sessile, solitary; apex of the microsporophyll a small triangular spur *c.* 0.2 mm long. *Seed-bearing structure* on a 8–16 mm peduncle; foliola 2–4 mm long; *receptacle* 10–11 mm long, formed of two unequal bracts, becoming red when mature. *Seed* with its covering, including a blunt apex, 9–11 by 7–8 mm.

Distr. *Malesia*: N. Sumatra (Gajo Lands: Kemiri & Bandahara Mts) and West New Guinea (Wissel Lakes). Fig. 53.

Ecol. In local forest populations, probably on poor soils, in N. Sumatra at 2500–3300 m, near Wissel Lakes at 1800 m.

5. Section Gracilis

DE LAUB. Blumea 30 (1985) 272.

Primary foliage bud small, up to 2 mm diam., but smaller in some species; primary scales erect or slightly spreading, triangular to lanceolate, up to 3 mm long and 1 mm wide at the base, only 0.6 mm wide in *P. glaucus*; secondary scales also acute, the secondary bud when it first appears a cluster of free bud tips. *Leaves* linear to ovate, acute to rounded at the apex, particularly delicate with remarkably blunt apices when growing in the shade, generally distinctly rigid when growing in exposed situations; midrib above distinct but gracile with sloping sides and about the size of an ordinary pencil line (up to 0.3 mm wide), broader and blunt to nearly flat below, three vascular resin canals. *Buds for pollen cones* sessile and quite small, the primary scales no more than 1.5 mm long with free tips; secondary scales about twice as long as broad, the secondary pollen cone bud when it first appears a spherical ball cupped by the primary scales. *Pollen cones* slender, mostly 2–3.5 cm long and *c.* 3 mm diam. before shedding pollen but 2–2.5 mm diam. after shedding, solitary, often elongating in the scaly base as well as in the zone of microsporophylls when mature. Apex of the microsporophyll a small triangular spur 0.3–0.5 mm long over a base *c.* 1 mm wide. *Seed-bearing structure* on a peduncle (3–)5–10(–16) mm long. Foliola 1.5 mm long. *Receptacle* formed of two bracts, the fertile bracts 7–8(–10) mm long, sterile bracts shorter, becoming red in some species and purple in others when mature. *Seed* with its covering globular, 7–8 mm long without a small crest and 8–9 mm long in species with a crest, mostly 5.5–6 mm diam. (less in *P. affinis* from Fiji).

Distr. From southern China through Malesia to Fiji, but not in Malaya, Sumatra, and Java, 5 *spp.* Two species widespread and the other three quite rare and outside the range of the other two. Four of the five species occur in the Philippines.

Ecol. Mossy mountain forests either on isolated peaks or at high elevation.

Note. A group of closely related species, some of which could conceivably be considered varieties inasmuch as certain variations of a like nature are also known within *P. pilgeri*. For example, *P. lophatus* has crowded leaves and a crest on the fruit, characters shared with *P. glaucus* but otherwise it corresponds with *P. pilgeri*. On the other hand, *P. wangii*, here included in *P. pilgeri*, has very small foliage buds and a purple ripe receptacle, characters also shared with *P. glaucus*.

KEY TO THE SPECIES

1. Leaves over 2 cm long; foliage bud at least 1.5 mm long.
 2. Leaves less than 8 mm wide, not always blunt (sun growth leaves acute).
  3. Leaves dispersed. Fruit not crested .... **18. P. pilgeri**
  3. Leaves crowded (overlapping). Fruit crested .... **19. P. lophatus**
 2. Leaves more than 8 mm wide, always blunt (dispersed; fruit not crested) .... **20. P. rotundus**
1. Leaves less than 2 cm long (less than 6 mm wide, always blunt, crowded); foliage bud less than 1.5 mm long (fruit crested) .... **21. P. glaucus**

18. Podocarpus pilgeri FOXW. Philip. J. Sc. 2 (1907) Bot. 259; *ibid.* 6 (1911) Bot. 160; PILGER, Bot. Jahrb. 54 (1916) 38; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; N.E.GRAY, J. Arn. Arb. 39 (1958) 459; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 185, t. 810; DE LAUB. Kalikasan 7 (1978) 135. — *P. celebica* (*non* HEMSL.) WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 78. — *P. costalis* (*non* PRESL) FOXW. Philip. J. Sc. 6 (1911) Bot. 161. — *P. schlechteri* PILGER, Bot. Jahrb. 54 (1916) 209; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; LAUT. Bot. Jahrb. 63 (1930) 474; PILGER, Bot. Jahrb. 68 (1936) 246; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 187. — *P. wangii* CHANG, Sunyatsenia 6 (1941) 26.

Tree 1–25 m tall, 8–60 cm diam.; bole to 12 m, rarely fluted. Foliage buds 2.5–3 mm long (or sometimes shorter). *Juvenile leaves* linear, up to 7 cm by 9 mm, broadly acute and apiculate. *Adult shade leaves* ovate, widest part closer to the apex, 2–4 cm by 5–8 mm, abruptly rounded at the apex, narrowing more gradually at the base to a short 2–3 mm petiole; exposed leaves elliptic, 2.5–4 cm by 4–6 mm, acute, revolute, with intermediate forms towards shade leaves common; midrib above on all leaves 0.2 mm wide and high. *Pollen cones* often elongating in the basal scaly part to 3 mm. *Female receptacle* becoming red when mature (dark violet has also been reported). *Seed* with its covering without a crest.

Distr. S. China; in *Malesia*: Philippines (Negros Occidental, Mindanao), Central Celebes, and common in New Guinea. Fig. 55.

Ecol. Scattered and locally common in moist and often mossy forest, (700–)1200–1300 m, as a medium-sized tree, but dwarfed on ridges and at high elevation. Mostly in the understory, in beech forest with mossy undergrowth, associated with *Phyllocladus* and *Myrsine*, in New Guinea in elfin woodland on Mt Hunstein and on Mt Nettoti in low *Xanthomyrtus-Podocarpus* crest forest.

Vern. West New Guinea: *bempop*, Hattam lang.; East New Guinea: *gihura*, Asaro, Kefamo, *iamugang*, Goroka, Togoba, *jamega*, Hagen, Togoba,

Fig. 55. Range of *Podocarpus pilgeri* Foxw.

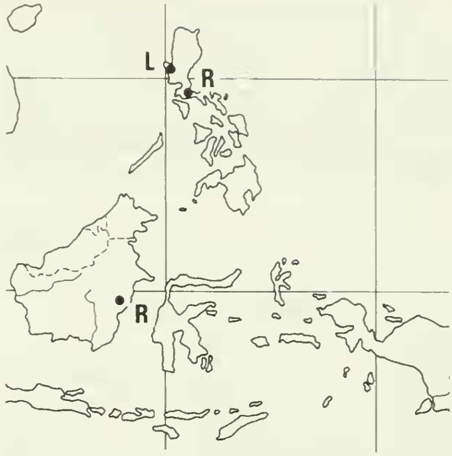

Fig. 56. Range of *Podocarpus lophatus* DE LAUB. (L) and *P. rotundus* DE LAUB. (R).

kaibeltugl, Wahgi, Minj, *kebu*, Mt Ne, *monopana*, Mairi, Natabung, *puling*, Hagen, Wankl, *sosumehi*, Dunantina, *sula*, Chimbu, Masul, *yamga*, Hagen, Minj, *yazib*, Nondugl, Minj.

Note. The great variability of the leaves can be confusing and the position on the tree of leaf collections should be noted.

19. Podocarpus lophatus DE LAUB. Kalikasan 7 (1978) 137. — *P. brevifolius* (*non* STAPF) FOXW. Philip. J. Sc. 6 (1911) Bot. 160, t. 29, f. 2; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) t. 801 p.p.

Small tree. Foliage buds 3 mm long. *Adult leaves* densely crowded, thick, elliptic, 3 cm by 5 mm, slightly revolute, acute, narrowed at the base to a short 2 mm petiole; midrib above a distinct ridge *c.* 0.2 mm wide. *Pollen cones* unknown. *Seed* with its covering with a distinct crest.

Distr. *Malesia*: Philippines (Luzon: Mt Tapulao), one locality only. Fig. 56.

Ecol. Mossy forest at 1800 m.

20. Podocarpus rotundus DE LAUB. Kalikasan 7 (1978) 136.

Tree 5–15 m tall. Foliage buds 2–3 mm long. *Juvenile leaves* linear, up to 10 cm long. *Adult leaves* oval to slightly linear, 2–5 cm by 8–11 mm, very rounded at the apex even when growing in exposed situations, sometimes apiculate, narrowed at the base to a 2 mm petiole; midrib above a small ridge 0.2 mm wide and high. *Pollen cone* elongating through the base to produce a scaly section 3–10 mm long. *Female receptacle* becoming red when mature. *Seed* with its covering without a crest.

Distr. *Malesia*: E. Borneo (Mt Beratus near Balikpapan) and Philippines (Luzon: Mt Banajao in Laguna Prov. and Lucban in Tayabas Prov.), 3 collections. Fig. 56.

Ecol. Dwarf mossy forest, on Mt Beratus at *c.* 1000 m, in Luzon up to 2200 m.

21. Podocarpus glaucus FOXW. Philip. J. Sc. 2 (1907) Bot. 258; *ibid.* 6 (1911) Bot. 159, t. 29, f. 1; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; WASSCHER, Blumea 4 (1941) 468; N.E.GRAY, J. Arn. Arb. 39 (1958) 440; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 163, t. 825; DE LAUB. Kalikasan 7 (1978) 138.

Decumbent shrub to small or medium-sized tree, 2–15 m tall, up to 20–25 cm diam. Foliage buds 1–1.5 mm long and 1.5 mm in diam.; primary budscales 0.6 mm wide. *Juvenile leaves* oval, 2–3.5 cm by 5–7 mm. *Adult leaves* ovate, the widest part somewhat beyond the centre, 1–2 cm by 3–6 mm, round and very blunt at the apex, narrowing at the base to a 2–3 mm petiole, revolute, crowded, flushing red, at least sometimes glaucous; midrib above a distinct ridge 0.2 mm wide. *Pollen cones* 1–2 cm long, often elongating in the basal scaly part to 1–2 mm. *Female receptacle* becoming purple when mature. *Seed* with its covering with a distinct crest.

Distr. Solomon Islands; in *Malesia*: New Guinea

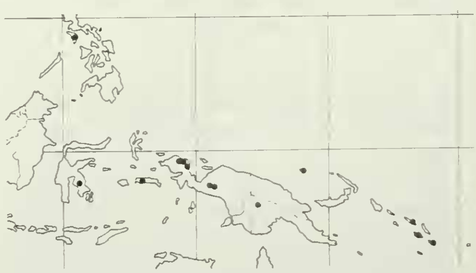

Fig. 57. Range of *Podocarpus glaucus* Foxw.

(also on Arfak Mts, and incl. Manus in Admiralty Is.), Moluccas (W. Ceram), and Philippines (Mindoro). Fig. 57.

Ecol. A medium-sized tree in the forest or more often dwarfed or even decumbent on mountain crests in stunted mossy forests, often locally common, (500–)1000–2800 m. Recorded from stony, sandy clay and from a limestone ridge associated with *Gymnostoma* and *Rhododendron*, near Kiunga and Wissel Lakes (New Guinea) on peaty soil.

Vern. West New Guinea: *nipa*, Kebar, *bèbiai*, Kapauko lang.

Note. Sterile young plants resemble *P. pilgeri*, but with crowded leaves.

6. Section Macrostachyus

DE LAUB. Blumea 30 (1985) 273.

Primary foliage bud mostly at least 4 mm diam. on vigorous shoots, but 3–3.5 mm diam. on weaker shoots, and generally somewhat smaller in some species, about as long as or somewhat longer than the diameter, none more than 5 mm long; primary scales triangular and erect or lanceolate and often with outwardly curling tips and thus longer than the bud itself; secondary scales acute or apiculate, the secondary bud when it first appears a nest of scale tips which elongates into a loose pyramid. *Mature leaves* only *c.* 5–8 mm wide and mostly less than 6 cm long, acute to rounded at the apex, narrowed gradually at the base, mostly revolute, tough, midrib above narrow but distinct, 0.2–0.4 mm wide and 0.1–0.2 mm high, broader and blunt below, sometimes drying to a channel, three vascular resin canals. *Buds for pollen cones* sessile (or in *P. crassigemmis* on a short peduncle), the secondary pollen cone bud when it first appears more exposed and still a globular ball. *Pollen cones* 2.5–5.5 cm long and up to 7 mm diam. before shedding pollen, but 4–5 mm diam. after shedding and even smaller in one variety which does not have the usual lanceolate 2–3(–4) mm apex of the microsporophyll, solitary or occasionally in pairs. *Seed-bearing structure* of various sizes, usually with a short peduncle 2–6 mm long and foliola *c.* 2 mm long; where known the fully ripe *receptacles* are dark purplish black passing through red in ripening.

Distr. In isolated populations from southern Cambodia and islands south of Taiwan to New Guinea, 5 *spp.*, of which 4 in *Malesia* (two widespread examples in New Guinea).

Ecol. Locally common at high elevations or on mossy ridges. One species, *P. costalis*, largely confined to a group of small islands at low elevation.

Note. A similar habitat and general distribution to *sect. Gracilis* but members of *sect. Macrostachyus* have robust leaves where those of *sect. Gracilis* are delicate. One sterile specimen from Sumatra (ICHLAS 166, Mt Singgalang, 2800 m) placed with *P. bracteatus* (*sect. Longifoliatus*), resembles *P. brevifolius* of the present section also, but more information is needed.

KEY TO THE SPECIES

1. Foliage bud at least 3 mm in diameter. Leaves elliptic.
   2. Seed with its covering not crested, more than 9 mm diameter.
      3. Leaf at least 7 times as long as wide. Pollen cone pedunculate .... **22. P. crassigemmis**
      3. Leaf less than 4 times as long as wide. Pollen cone sessile .... **23. P. brassii**
   2. Seed with its covering crested, less than 8 mm diameter. (Leaf less than 7 mm wide) **24. P. brevifolius**
1. Foliage bud less than 3 mm in diameter. Leaves more or less linear blunt. (Fruit crested, less than 7 mm diameter)... **25. P. costalis**

22. Podocarpus crassigemmis DE LAUB. Blumea 26 (1980) 141. — *P. archboldii* (*non* N.E.GRAY) GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 177, t. 828; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 30, t. 41.

Tree (3–)8–38 m tall, 10–75 cm diam., bole occasionally fluted. Sometimes pagoda habit. Foliage buds 3–5 mm long, the primary scales up to 8 mm long, on juvenile plants to over 10 mm, strongly curling outward. *Juvenile leaves* linear-lanceolate, narrowly acute, up to 20 by 1.4 cm. *Adult leaves* elliptic, 3–11 cm by 4.5–12 mm, acute to narrowly acute, narrowing at the base to a 2–5 mm petiole, revolute, midrib above a sharp ridge 0.2–0.4 mm wide and 0.2 mm high. Buds for pollen cones on a 1–7 mm peduncle, primary scales up to 4.5 mm long. *Pollen cones* occasionally in pairs. *Seed-bearing structure* on a 5–14 mm peduncle; *receptacle* 10–15 mm long. *Seed* with its covering 11–14 by 9–10 mm.

Distr. *Malesia*: New Guinea (except Vogelkop Peninsula). Fig. 58.

Fig. 58. Range of *Podocarpus crassigemmis* DE LAUB.

Ecol. Common or subdominant in the canopy of high mountain mossy forest, or emergent, often in *Nothofagus* and *Phyllocladus* forest, rarely in secondary forest and occasionally in grassland, (1800–)2100–3400 m.

Vern. East New Guinea: *a-pul, kaboga, morumba*, Mt Giluwe, Mendi lang., *baula*, Kundiawa, Chimbu, *iamuka*, Tomba, *jamekang*, Hagen, Tomba, *juba, kamga, puling*, Hagen, Togoba, *kabor*, Anga Valley, Mendi lang., *kabiltugl, kaibelparu, kaibig*, Wahgi, Minj, *kaip*, Kepilam, Enga lang., *nonofan*, Mairi, Watabung, *ronohanini*, Asaro, Kefamo, *(t)sula*, Chimbu, Masul.

Note. Leaves from lower parts of trees substantially larger than those from higher or more exposed parts of the same tree can at the same time bear fertile material.

In the Goroka Subdistrict STEVENS found two trees (LAE 51011) of which the leaves were infected with *Corynelia uberata* FRIES, widely distributed in the Old World.

23. Podocarpus brassii PILGER, Bot. Jahrb. 68 (1937) 246; WASSCHER, Blumea 4 (1941) 469; N.E.GRAY, J. Arn. Arb. 39 (1958) 440; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 163, t. 824; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 24, t. 37, 38.

KEY TO THE VARIETIES

1. Apex of microsporophyll lanceolate, at least 2 mm long. Tree .... **a.** *var.* **brassii**
1. Apex of microsporophyll triangular, less than 1 mm long. Small tree to prostrate shrub **b.** *var.* **humilis**

a. *var.* **brassii**

Tree 3–30 m tall, up to 75 cm diam. Foliage buds 4–5 mm long, primary scales erect and up to 5 mm (or more) long. *Juvenile leaves* linear, 2.5–4 cm by 5–7.5 mm, acute or even apiculate, narrowing abruptly at the base. *Adult leaves* oval, 1–2.5 cm by 4–7 mm, broadly acute, narrowing more or less abruptly at the base to a 1–2 mm petiole, revolute, glaucous on the underside; midrib above a sometimes indistinct ridge 0.2 mm wide and 0.1 mm high. *Pollen cone* 6–7 mm diam.; apex of the microsporophyll lanceolate or slightly rounded at the tip, 3–4 mm long. *Seed-bearing structure* on a 1–9 mm peduncle; *receptacle* 6–9 mm with the apex of the otherwise adnate bracts spreading. *Seed* with its covering 10–13 by 9 mm.

Distr. *Malesia*: New Guinea (except Vogelkop Peninsula). Fig. 59.

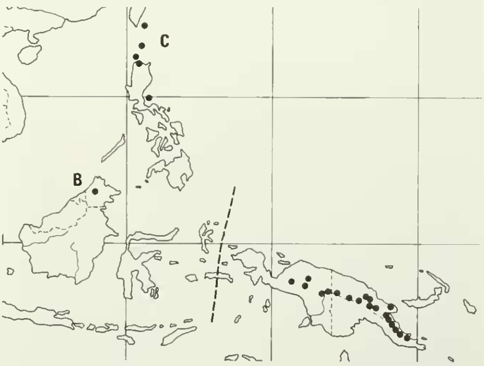

Fig. 59. Range of *Podocarpus brassii* PILGER (east of line), *P. brevifolius* (STAPF) FOXW. (B), and *P. costalis* PRESL (C).

Ecol. Common and sometimes dominant near the tree line, often an emergent in alpine scrub, often flat-topped, also a gnarled treelet in fire-induced grasslands or in coppices on edge of grassland, on limestone fields, rarely in mossy forest, commonest between 3000 and at least 3750 m, but also occasionally lower: Mt Ambua 2600 m, Ibiware 2700 m, Wissel Lakes 2000 m.

Vern. East New Guinea: *bacela*, Kundiawa, Chimbu, *baugwa*, Waimambano, Chimbu, *chuga*, Chimbu dial., *kaibigl-tuga, ra*, Kubor, Minj, *kaipil*, Wahgi, Minj, *maja*, Mairi, Mondo, *tsulo*, Masul, Chimbu.

b. *var.* **humilis** DE LAUB. Blumea 30 (1985) 274.

Decumbent shrub to small tree up to 5 m high. *Pollen cones* 3.5–4.5 mm diam.; apex of the microsporophyll triangular, 1 mm long.

Distr. *Malesia*: New Guinea (except Vogelkop Peninsula). Fig. 59.

Ecol. High elevation scrub, 2600–3600 m, prostrate in open areas, sometimes with pools, on Mt Capella forming dense mats 3 m square, 15–30 cm high.

Note. Definitely not a stunted alpine form, being found at lower elevations than the other (larger) variety which actually occurs as a tree in the alpine scrub at or near the tree line. Only the pollen cone and the prostrate habit that often develops distinguish the two varieties so that herbarium specimens cannot always be assigned with confidence to their proper variety.

24. Podocarpus brevifolius (STAPF) FOXW. Philip J. Sc. 6 (1911) Bot. 160, t. 29, f. 2; PILGER, Bot. Jahrb. 54 (1916) 40; WASSCHER, Blumea 4 (1941) 466; N.E.GRAY, J. Arn. Arb. 39 (1958) 441; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 165, t. 801, *p.p.* — *P. neriifolius var. brevifolius* STAPF, Trans. Linn. Soc. Bot. 11, 4 (1894) 249.

Small, often gnarled, sometimes conical tree 2–7.5 m tall. Foliage bud 3.4–4 mm long, primary scales erect, spreading at their tips, occasionally somewhat longer than the bud itself. *Juvenile leaves* 5–8 cm by 6–9 mm, narrowly acute. *Adult leaves* elliptical, 2–5 cm by 4–6.5 mm, acute, narrowed at the base to a broad 1–2 mm petiole, slightly revolute; midrib above a narrow ridge 0.2 mm wide and 0.1 mm high. *Seed-bearing structure* on a 2–4 mm peduncle; foliola *c.* 3 mm long; receptacle 6–8 mm long. *Seed* with its covering 10–12 (including a small crest) by 6.5 mm.

Distr. *Malesia*: N. Borneo (Sabah: Mt Kinabalu). Fig. 59.

Ecol. Scattered and locally common in or under dwarf forest, (2100–)2650–3750 m, on granite rocks.

Note. Reports of occurrences in various other places have all proven to be distinctly different species.

25. Podocarpus costalis PRESL, Epim. Bot. (1849) 236; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 78; FOXW. Philip J. Sc. 6 (1911) Bot. 161, *p.p.*; N.E.GRAY, J. Arn. Arb. 39 (1958) 456; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 183, t. 831. — *P. polystachyus* (*non* R.BR.) LI & KENG, Taiwania 5 (1954) 34, t. 5; LI, Woody Fl. Taiwan (1963) 41, f. 5; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) t. 812, *p.p.*

Small tree *c.* 1–5 m high, possibly higher. Foliage buds 2–4 mm long, primary scales erect. *Juvenile leaves* up to at least 9 by 1.3 cm, acute or more or less rounded at the apex. *Adult leaves* linear, 4–7 cm (or as little as 2.5 cm on short side branches) by 5–10 mm, broadly acute or more usually rounded at the apex, sometimes with a small blunt apiculus, narrowing more or less abruptly at the base to a 2–3 mm petiole, slightly revolute; midrib above a distinct ridge 0.3 mm wide and 0.2 mm high. *Seed-bearing structure* on a 4–6 mm peduncle; foliola *c.* 1.5 mm long and early caducous; *receptacle* 12–15 mm long, reported to be red when mature. *Seed* with its covering 9–10 (including a small crest) by 6–7 mm.

Distr. S. Taiwan (Orchid I.); in *Malesia*: Philippines (N. Luzon, on Bucas and other isles between Luzon and Taiwan and possibly on the northcoast of Luzon). Fig. 59.

Ecol. Coastal bluffs near sea-level to at least 300 m.

Note. Popular in cultivation in the Philippines and often confused with *P. polystachyus* because of a similar habitat and similar sized leaves. The leaves of *P. costalis* are slightly revolute while those of *P. polystachyus* are not.

7. Section Rumphius

DE LAUB. Blumea 30 (1985) 274.

Primary foliage bud globular, up to 4 mm long; primary scales as long as the bud, triangular, crowded together more or less into a pyramid usually with the very tip of some or all of the scales bent away from the apex of the pyramid; secondary scales acute to slightly acuminate, the secondary bud when it first appears in most cases a spherical ball as in *sect. Globulus* but in *P. laubenfelsii* the scale tips may already be free. *Leaves* linear, sometimes larger than average for the genus, acute or on juvenile specimens sometimes slightly acuminate, narrowing more or less abruptly at the base to a 4–16 mm petiole, stiff, mostly with a continuous upper hypoderm, midrib blunt above, at least 0.7 mm wide, broader and sometimes almost flat below, usually three vascular resin canals. *Buds for pollen cones* 1.5–2 mm long, either sessile or on a short peduncle, the primary scales 1–1.5 mm wide at the base; secondary scales rounded, the secondary pollen cone buds when they first appear a round ball of overlapping imbricate scales. *Pollen cones* 2 to at least 4 cm long, usually in groups of more than three. Apex of the microsporophyll a small triangular spur 0.2 mm long over a wider base. *Seed-bearing structure* on a (2.5–)6–16 mm peduncle; foliola 1–1.5 mm long; *receptacle* mostly formed of two bracts, the longer fertile one 9–15 mm long or both fertile and equal, in *P. rumphii* a third lateral smaller bract often found; where known the ripe receptacle becomes red. *Seed* with its covering globular, at least 8 mm long, larger in *P. rumphii.*

Distr. One very widespread species from the fringes of Asia through New Guinea and two localized species, one in northern Borneo and the other in northern Queensland. In *Malesia* 2 *spp.*

Ecol. Scattered, often widely separated stands involving large, primary rain-forest canopy trees at generally low elevation.

Note. A transitional section which shares multiple clustered pollen cones with *sect. Polystachyus*, but lacks the purple fruit of that section and shares the spherical developing pollen cone buds with *sect. Globulus* along with generally broad and blunt upperside of the midribs. The ecology and large linear leaves are somewhat distinct.

KEY TO THE SPECIES

1. Pollen cones sessile; foliage budscales often completely adpressed; receptacle often with a third lateral smaller sterile bract .... **26. P. rumphii**
1. Pollen cone clusters usually on a small peduncle; foliage budscales always spreading at the tips; receptacle never with a third lateral sterile bract .... **27. P. laubenfelsii**

26. Podocarpus rumphii BLUME, Rumphia 3 (1849) 214; MIQ. Fl. Ind. Bat. 2 (1859) 1073; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 393; DE BOER, Conif. Arch. Ind. (1866) 15; PARL. in DC. Prod. 16, 2 (1868) 515; BECC. Malesia 1 (1877) 179; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 104; WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 81; FOXW. Philip. J. Sc. 2 (1907) Bot. 258; MERR. Interpr. Rumph. (1917) 75; FOXW. Philip. J. Sc. 6 (1911) Bot. 164; WASSCHER, Blumea 4 (1941) 432; N.E.GRAY, J. Arn. Arb. 39 (1958) 455; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 179, t. 815; DE LAUB. Blumea 24 (1978) 496; Kalikasan 7 (1978) 141. — *Nageia rumphii* (BLUME) F.v.M. Descr. Not. 1 (1877) 93. — *P. koordersii* PILGER *ex* K. & V. Bijdr. Booms. 10 (1904) 268; KOORD. Exk. Fl. Java 1 (1911) 66; K. & V. Atlas Baumart. Java 3 (1915) t. 587; WASSCHER, Blumea 4 (1941) 431; N.E.GRAY, J. Arn. Arb. 39 (1958) 433; BACKER & BAKH. *f.* Fl. Java 1 (1963) 90; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 159, t. 804. — *P. philippinensis* FOXW. Philip. J. Sc. 6 (1911) Bot. 163, t. 30; N.E.GRAY, J. Arn. Arb. 39 (1958) 434; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 159.

Tree 12–45 m tall, up to 35–75 cm diam. Foliage buds 2.5–4 mm long, the tips of the primary scales meeting at the apex with one or two often bent outward at the tip. *Juvenile leaves* 19–26 by 1.9–2.6 cm, acute or slightly acuminate. *Adult leaves* on smaller trees and lower branches of taller trees linear, 12–22 by 1.1–1.9 cm, acute or slightly acuminate, narrowing distinctly at the base to a 4–16 mm petiole, stiff; leaves from the exposed parts of taller trees 9–14 cm by 9–14 mm, acute, with a 4–10 mm petiole; upper side of midrib of all leaves a blunt ridge 0.7–1.2 mm wide and 0.3 mm high, often collapsing when dried to a flat surface or a small irregular ridge. Buds for pollen cones sessile. *Pollen cones* in groups of up to at least five, 3.5–4.5 cm long; microsporophylls somewhat elongated and tightly crowded. *Receptacle* frequently with a third lateral bract smaller than the other two. *Seed* with its covering glaucous, 12–15 by 10–12 mm.

Distr. Hainan; in *Malesia*: Malaya (Genting Highl.), S. Central Java (Nusa Kambangan), Bawean I. (Java Sea), Borneo (Sabah, incl. Selangan Is.), Philippines (Luzon: Agusan del Norte), Celebes, Lesser Sunda Islands (Flores, Timor) Moluccas (Obi, Weda, Aru Is.), New Guinea (incl. Misool & Numfoor Is.). Fig. 60.

Ecol. Locally common in primary rain-forest but rather in widely separate localities, frequently on islands, in Java on limestone, 5–200(–600–1550) m.

Uses. Reported to be a good timber tree.

Fig. 60. Range of *Podocarpus rumphii* BLUME.

Vern. Borneo: *kayu china*, Sabah, Selangan; Philippines: *malakanayan*, Luzon, Agusan; Celebes: *sandu*, Malili; Lesser Sunda Islands: *mermolas, moak*, Flores, *e-tama*, Timor, Bunaq lang.; Moluccas: *kayu china, rangundjela*, Aru Is., P. Wokam; West New Guinea: *aibemmunowame, aiwimunwame*, Fakfak, Biak lang., *eswasa, weswaze*, Arguni Bay, Irahutu lang., *manulit*, Misool I., *onen*, Warsamson R., Mooi lang., *osien*, Sorong, Mooi lang., *djèra, si-èra*, Mimika, *wasabraran*, Numfoor, Biak lang.

Note. Generally homogeneous throughout its range but the transition from large juvenile to small adult leaves mostly takes the form of long slender leaves towards the west and shorter broader leaves further east, especially in the Aru region. The Aru specimens apparently lack the usual continuous upper hypoderm as well.

27. Podocarpus laubenfelsii TIONG, Blumea 29 (1984) 523.

Tree, 14–35 m tall, 20–60 cm diam. Foliage buds 2.5–4 mm long, the tips of the primary scales generally spreading. *Juvenile leaves* 11–24 by 1.7–2.4 cm. *Adult leaves* linear to linear-lanceolate, 7–19 by 1–1.8 cm, narrowly acute to acuminate, narrowing more or less abruptly at the base to a 6–14 mm petiole, upper side of midrib a blunt ridge 0.8–1.2 mm wide and 0.2–0.3 mm high. Buds for pollen cones on a peduncle to 6 mm long or less commonly sessile. *Pollen cones* grouped (3) 4 (5), 2–4 cm long; microsporophylls more or less elongated. *Seed* with its covering at least 8 mm long but fully mature examples unknown.

Distr. *Malesia*: Borneo (Sarawak: Lawas; Sabah: Trusmadi & Kinabalu; E. Kalimantan: Kutei). Fig. 61.

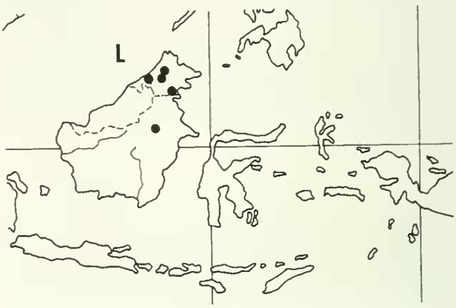

Fig. 61. Range of *Podocarpus laubenfelsii* TIONG.

Ecol. Scattered in primary rain-forest, in mossy forest, a large emergent on rocky ridge on kerangas, dominant in heath forest, also in waterlogged acid soil of *Agathis* forest. 600–1600 m.

8. Section Polystachyus

DE LAUB. Blumea 30 (1985) 275.

Foliage bud on vigorous shoots mostly 2–2.5 mm diam. and on weaker shoots 1–1.5 mm diam., larger in *P. macrocarpus*, up to 4.5 mm long in species with more or less linear leaves and 4–9 mm long in species with distinctly lanceolate leaves; primary foliage budscales erect, sometimes slightly spreading, triangular to lanceolate, up to 1.5 mm wide at the base in vigorous buds and 1 mm wide in weaker buds; secondary budscales more or less rounded or slightly acuminate, the secondary bud when it first appears a cluster of scale tips or when with particularly short primary scales may still be more or less in a ball. *Leaves* linear and almost blunt to lanceolate, sometimes in the same species at different stages of growth; midrib prominent above, usually less than 0.6 mm wide, broader and blunter below, usually three vascular resin canals but occasionally more (or less). *Buds for pollen cones* up to 3 mm long, either sessile or on a short peduncle; the secondary pollen cone buds when they first appear a round ball of overlapping scales. *Pollen cones* variable in length among the species but most commonly 2–4 cm long, normally in clusters of up to five; apex of the microsporophyll similarly variable in length but most commonly a small spur 0.2–0.3 mm long over a wider base. *Seed-bearing structure* on a variable-sized peduncle, mostly 3–12 mm long but shorter in some species; foliola mostly 1.5–2 mm long; *receptacle* normally formed of two unequal bracts with one fertile but occasionally both are fertile and equal, the fertile bracts mostly 7–12 mm long (longer in *P. fasciculus*), in most species known to become purple after passing through red when ripening. *Seed* with its covering of various sizes, globular and blunt.

Distr. Central China and southern Japan through Malesia to eastern Australia, 9 *spp.* Most of these species occur in or near China. In *Malesia* 3 *spp.*

Ecol. Scattered in (subtropical and) highland tropical forests but one species occurs on tropical sandy coastal bluffs or low elevation limestone outcrops.

Note. In two species only pink ripe receptacles have been reported but in this section just as in familiar *Rubus* fruits, a crop of pink or red fruit is later seen to become purple or in other cases fruit bats strip off the fully ripe fruit leaving only the less ripe red, so reports of red or pink may not be conclusive. Isolated specimens may well have pollen cones in clusters of no more than 3 but a normal flush of pollen cone production will have larger clusters well represented and collectors should note this.

KEY TO THE SPECIES

1. Adult leaves linear and more or less rounded at the apex, not lanceolate, upper midrib prominent.
 2. Seed and its covering less than 8 mm in diameter. Midrib above sharp .... **28. P. polystachyus**
 2. Seed and its covering more than 10 mm in diameter. Midrib above blunt .... **29. P. macrocarpus**
1. Adult leaves lanceolate, narrowly acute at the apex, upper midrib indistinct .... **30. P. ridleyi**

28. Podocarpus polystachyus R.BR. *ex* ENDL. Syn. Conif. (1847) 215; MIQ. Fl. Ind. Bat. 2 (1859) 1072; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 392; PARL. in DC. Prod. 16, 2 (1868) 515; WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 79; MERR. Philip J. Sc. 3 (1908) Bot. 394; FOXW. Philip. J. Sc. 6 (1911) Bot. 161; RIDLEY, Fl. Mal. Pen. 5 (1925) 282, t. 228; WASSCHER, Blumea 4 (1941) 456, t. 5, f. 14a–c; N.E.GRAY, J. Arn. Arb. 39 (1958) 469, f. 4; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 49, f. 3, *p.p.*; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 191, t. 812, *p.p.*; DE LAUB. Kalikasan 7 (1978) 142. — *P. neriifolius* D.DON in Lamb., Pinus 1 (1824) 21, *p.p.*; HOOK. *f.* Fl. Brit. India 5 (1888) 649, *p.p.* — *P. thevetiifolia* BLUME, Rumphia 3 (1849) 213; MIQ. Fl. Ind. Bat. 2 (1859) 1074; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 397; DE BOER, Conif. Arch. Ind. (1866) 22, t. 2; PARL. in DC. Prod. 16, 2 (1868) 518; BECC. Malesia 1 (1877) 180; WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 79; WASSCHER, Blumea 4 (1941) 462; N.E.GRAY, J. Arn. Arb. 39 (1958) 457; BACKER & BAKH. *f.* Fl. Java 1 (1963) 90; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 183, t. 829. — *Nageia thevetiaefolia* (BLUME) F.v.M. Descr. Not. Pap. Pl. 1 (1877) 93. — *Nageia polystachyus* (R.BR. *ex* ENDL.) O. K. Rev. Gen. Pl. 2 (1891) 800. — **Fig. 62.**

Tree 1–20 m tall, 3–45 cm diam., most commonly *c.* 6 m. Foliage buds 1.5–3 mm long. *Juvenile leaves* generally within the upper range of adult leaf size, linear to linear-lanceolate, acute and almost

Fig. 62. *Podocarpus polystachyus* R.BR. *ex* ENDL. Pollen cones, ×1.4 (Photogr. A.ELSENER, 1965).

apiculate, sometimes mixed with more typical adult leaves. *Adult leaves* linear to oval, 3–10 cm by 6–13 mm, more or less acute to rounded at the apex, narrowed abruptly at the base to a 1–3 mm peduncle, margin flat or nearly so; midrib above a sharp ridge 0.3–0.4 mm wide and 0.2 mm high. Buds for pollen cones sessile. *Pollen cones* 2–4 cm long, clustered in groups of up to at least five. *Seed-bearing structure* on a 1–6 mm peduncle; foliola 1–1.5 mm long, falling; *receptacle* 7–10 mm long. *Seed* with its covering 7–9 by 5–7 mm.

Distr. Southernmost Peninsular Thailand; in *Malesia*: Malay Peninsula, Riouw-Lingga & Banka Is., Borneo (W. Kalimantan: Pasir Pandjang & Karimata I.; Sarawak; Brunei; Sabah), Philippines (Palawan; Luzon: Tayabas & Ilocos Norte Prov.), Moluccas (Obi, Waigeu), West New Guinea (Vogelkop Peninsula). Fig. 63.

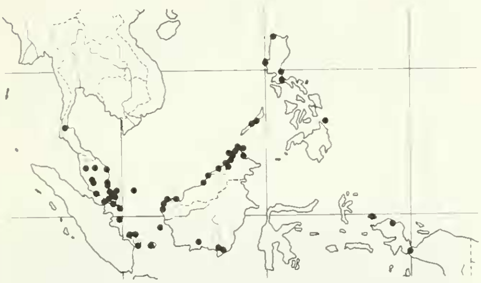

Fig. 63. Range of *Podocarpus polystachyus* R.BR. *ex* ENDL.

Ecol. The main occurrences are at low altitudes and fall apart for the major part into three ecologies. First, the principal habitat is sandy beaches, often gregariously bordering the sea at hightide mark and sandy coastal bluffs and low outcrops, also mentioned for sandy ridges in the mangrove. On coastal granite and limestone rocks the trees are gnarled. Second, it is often frequent on lowland coastal kerangas and sandy 'pandangs' (degraded heath forest) and sandy heath forest (Menchali For. Res., Pahang). These two habitats are typical in the Sunda Land. Third, on limestone hills inland, for instance in Malaya and the Philippines, in Obi, Waigeu, and the Vogelkop Peninsula in New Guinea at 180, 280 and 550 m, at 1000 m in Palawan. In East Malesia these occurrences are scattered.

The bole is sometimes recorded to be fluted. The tree is found in Obi exceptionally tall, 40 m, with a clear bole of 25 m and 38 cm diam., and buttresses of 1 by 1.5 m. A most interesting ecology.

Vern. Malaya: *jati bukit*, Selangor; Lingga: *kayu karamat*; Borneo: W. Kalimantan: *mayu serai*, Bt. Besar, *tentada*, Matan; Sarawak: *landin*, Bintulu; Brunei: *anggeriting*; Sabah: *kandabang*, Bajau l'tan, *kayu china*, Sibuboh For. Res., *saumah*, Manadahan; New Guinea: Vogelkop: *arbudjin*, Maibrat lang., *rabudien*, Lake Ajamaru.

Note. Often cultivated (*e.g.* in Medan in gardens and parks) and remarkably similar to the also widely cultivated *P. macrophyllus* whose native range and ecology nevertheless is quite distinct. The leaves of *P. macrophyllus* usually have narrow but definitely revolute margins which narrow gradually towards the base while the leaves of *P. polystachyus* are not revolute and narrow abruptly at the base. GRAY (1958) reported that the leaves of *P. polystachyus* have upper hypodermal fibres 70 µm diam., while in *P. macrophyllus* these are less than 20 µm.

29. Podocarpus macrocarpus DE LAUB. Kalikasan 7 (1978) 140.

Tree 10–20 m tall, up to 30 cm diam. Foliage buds 2–4 mm long and the same in diameter; the longer buds with distinctly spreading upper parts of the primary scales; the secondary bud when it first appears may still be a globular ball with the shorter examples of primary budscales. *Juvenile leaves* linear-lanceolate, 8–15 by 1–1.4 cm, acute. *Adult leaves* linear to linear-lanceolate, 6–10 cm by 8–13 mm, acute but often slightly rounded at the apex, narrowed at the base more or less to a 2–4 mm petiole, thick with nearly continuous upper hypoderm and more or less shiny on the upper surface; midrib above a blunt ridge 0.5–0.6 mm wide and 0.2–0.3 mm high. Buds for pollen cones sessile. *Pollen cones* 2.5 cm long, grouped in clusters of up to at least four. *Seed-bearing structure* on a 3–12 mm peduncle; *receptacle* 10–12 mm long. *Seed* with its covering 15–17 by 10–13 mm.

Distr. *Malesia*: Philippines (northern Luzon). Fig. 64.

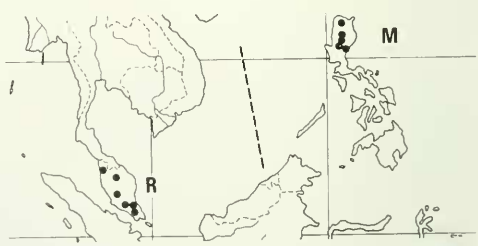

Fig. 64. Range of *Podocarpus macrocarpus* DE LAUB. (M) and *P. ridleyi* (WASSCHER) N.E.GRAY (R).

Ecol. Scattered and sometimes common in cloud forests, *c.* 2000–2100 m. One collection reported at 700 m is doubtful.

30. Podocarpus ridleyi (WASSCHER) N.E.GRAY, J. Arn. Arb. 39 (1958) 435; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 159, t. 814. — *P. neriifolius var. ridleyi* WASSCHER, Blumea 4 (1941) 453; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 49, f. 3, *p.p.*

Tree 4–24 m tall, 20–30 cm diam. Foliage buds 4–8 mm long. *Juvenile leaves* linear-lanceolate, 11–20 by 1.1–1.6 cm, narrowly acute. *Adult leaves* linear-lanceolate to lanceolate, 5–12 cm by 7–14 mm, acute, narrowed at the base more or less to a 2–3 mm petiole, slightly revolute, with a continuous upper hypoderm, sometimes with five vascular resin canals; midrib above a low ridge 0.2–0.5 mm wide and 0.1–0.2 mm high. Buds for pollen cones sessile or on a 1 mm peduncle. *Pollen cones* 1.5–2 cm by 2 mm, clustered to at least four; apex of the microsporophyll a tiny triangular spur 0.1 mm long. *Seed-bearing structure* on a 3–12 mm peduncle; *receptacle* 8–9 mm long, known to turn pink. *Seed* with its covering 7 by at least 4 mm.

Distr. *Malesia*: Malay Peninsula. Fig. 64.

Ecol. Localized and more or less dominant on several isolated peaks with poor soils in a somewhat stunted rain-forest, 480–1300 m. On ridge in Panti For. Res. over standstone, on Mt Ophir on granite.

ARAUCARIACEAE

Monoecious, medium-sized to very large trees (rarely shrubby in very exposed situations). Either four independent *cotyledons* or two fused pairs (which may be retained in the seed after germination). The growing point of foliage shoots quite distinct between the two genera, being just a few highly reduced leaves in *Araucaria* and a highly organized bud formed of overlapping scales in *Agathis*. The leaves vary from scales or needles to broad leathery forms with many parallel veins sometimes on the same plant at different stages of growth. *Pollen* produced in cylindrical cones from one to as much as twenty cm long with numerous pedunculate spirally placed microsporophylls each with several to many pendent elongated pollen sacs attached to the lower side of an enlarged shield-like apex which also projects apically more or less overlapping the adjacent microsporophylls. *Pollen cones* solitary, terminal or lateral, on branches separate from those bearing seed cones, subtended by a cluster of more or less modified leaves in the form of scales, deciduous when mature. Pollen globular, without 'wings'. *Seeds* produced in large, well-formed cones which disintegrate when mature, dispensing the seeds in most cases with the help of wing-like structures; the seed cone terminal on a robust shoot or peduncle with more or less modified leaves that change in a brief transition zone at the base of the cone into cone bracts, formed of numerous spirally-placed bract complexes, usually maturing in the second year. Individual seed cone bract leathery or woody and fused with the fertile scale which bears one large inverted seed on its upper surface.

Distribution. The 40 species in two genera are well represented in *Malesia* (13 *spp.*) and extend eastward and southward into Fiji, New Caledonia (18 *spp.*), Australia, and New Zealand, with 2 *spp.* also in the cooler parts of South America, giving the family a distinct Antarctic relationship. Only one species of *Araucaria* (in South America) occurs completely outside of the tropics, while the majority of the species in the family belong in the lowland tropics and others grow in the tropical highlands.

Fossils. Early coniferous fossils are often characterized as 'Araucarioid' because of the morphological resemblance of fossil foliage shoots to certain well-known juvenile forms of *Araucaria*, but there is no reason to conclude that these actually belong in *Araucariaceae*. Acceptable fossils of *Araucariaceae*, however, from Jurassic and Cretaceous age are well represented in the general areas of their modern occurrences, often at higher latitudes to be sure, and also in India and South Africa. More surprising is the apparent occurrence of fossils belonging to the family during the same time span but far away in North America and Europe (FLORIN, 1963; GAUSSEN, 1970). A close relationship of English Jurassic fossils specifically to *Araucaria bidwillii* is indicated by STOCKEY (1981). Wherever the family may have originated, it became well established in the southern hemisphere in Mesozoic times and has since disappeared from whatever northern occurrences it may have had. The genus *Agathis* is first recorded in the Oligocene of Australia and New Zealand and today extends into the Asian tropics, while no convincing fossils have ever been found in any other part of the world for this genus.

Tertiary records of the two modern genera of *Araucariaceae* are all well south of the equator across all of the southernmost land areas including the Palmer Peninsula of Antarctica. Speculation about tropical origins or early penetration of the tropics is not supported by any evidence and it is at least as likely that the occupation of the Malesian region took place during Plio-Pleistocene times alongside advancing members of *Podocarpaceae*.

Maps of fossil distributions are given in FLORIN (1963).

References: FLORIN, Acta Horti Berg. 20 (4) (1963) 121–312, 68 maps; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 42–56, f. 555–558; MACARTHUR, The genus *Araucaria* in its geographical aspects, Univ. W. Austr., Geogr. Lab. Econ. Dept., Research Rep. 5 (1949); STOCKEY, Canad. J. Bot. 59 (1981) 1932–1940.

Ecology. Canopy trees or emergents of moist forests at a wide range of elevations starting at sea-level in the tropics and extending to tropical highlands and to intermediate elevations in the middle latitudes. (One species in New Caledonia grows in drier forests and open places.) Some species clearly follow disturbances and others just as clearly do not. Many contrasting soil types are associated with different species.

Most or probably all species are monoecious and pollination is by wind. Frequent reports of dioeciousness result from a single sex stage, inasmuch as many species produce seed cones well before pollen cones appear. Dense stands are common for many but by no means all species and the large amounts of pollen are adequate to reach substantial distances effectively. Seeds are carried only short distances by wind in most cases and germinate in large numbers near their parent tree. The occurrence of isolated specimens shows that seeds sometimes are carried across substantial distances.

Growth occurs in distinct episodes and where distinct terminal buds are not evident whole units of growth tend eventually to be shed as a unit. Leaves normally persist for several years and may be shed separately from branch units in some cases. Cyclic growth results in false whorls of branches and a tendency for highly formal tree architecture.

A number of pests and diseases specific and otherwise of *Agathis* have been reported by WHITMORE (1977) mostly outside of Malesia. In particular a moth genus, *Agathiphaga*, specifically attacks cones, while a coccid, *Coniferococcus agathidis*, causes defoliation. Problems mostly arise when normally dispersed trees are concentrated in plantations. GAUSSEN (1970: 62 & 66) lists a variety of pests of *Araucaria*, mostly associated with cultivated examples. Notable are a 'pine bark weevil' (*Aesiotes notabilis*) and the 'hoop pine borer' (*Calymmaderus*). Termites of the genus *Coptotermes* do serious damage to *A. hunsteinii*.

Embryology. The fertilized egg undergoes at least five mitoses resulting in 32 or more free nuclei before cell walls form. The resulting cluster of cells deep inside the egg (proembryo) is then organized into three parts. The cells closest to the archaegonium elongate to form a massive 'prosuspensor' while those on the opposite side form a temporary 'cap'. The cells at the centre of the proembryo become the embryo proper, which does not undergo cleavage as in many other conifers. Simple polyembryony resulting from more than one fertilized archaegonium, however, may occur. The large number of proembryo cells and the massive embryonic 'cap' are distinct for

Araucariaceae within the conifers. The chromosome number is n = 13. No hybridization is suspected.

Taxonomy. Two well marked genera are recognized.

Uses. The large size of individuals in many species in this family along with the excellent quality of the wood has made them prime candidates for lumber production where sufficiently dense stands occur. The wood is light coloured, yellowish or brownish, straight grained, easily worked, durable, and generally similar to pine but somewhat harder than the more familiar types. The wood is sometimes intermingled and hardly distinguishable from material of *Podocarpaceae*. Important stands of *Agathis* have been exploited in Borneo and stands of *Araucaria* in New Guinea (ISMAIL, 1964; GRAY, 1975; HAVEL, 1971), as well as many locations outside of Malesia. Heavy exploitation has reduced the economic importance of this family. Some attempts have been made to establish tree plantations, but this effort is in the early stages of development (WHITMORE, 1977, 1980; BOWEN & WHITMORE, 1980). Large quantities of pitch have been gathered, particularly from certain species of *Agathis* where it is known as 'dammar'. Both fossil pitch with darker colours and fresh pitch which is much lighter have been produced. Immense dammar trees sometimes have some form of steps built into their trunks to enable collectors to reach the accumulating pitch. Specimens of various species make handsome ornamentals and are widely used in landscaping in the warmer parts of the world. (The seeds of several *Araucaria* species are in great demand as food.)

References: BOWEN & WHITMORE, Commonw. For. Rev. 59 (1980) 307; B.GRAY, J. Ecol. 63 (1975) 273–289; HAVEL, J. Ecol. 59 (1971) 203-213; ISMAIL BIN HAJI ALI, Mal. For. 27 (1964) 354–360; WHITMORE, A first look at *Agathis*, Oxford (1977); Econ. Bot. 34 (1980) 1.

Note. The great size of trees in this family has led to an emphasis on collection of juvenile foliage specimens and immature cones and when this is not admitted by the collectors the result can be misleading. Because the seed cones shatter on maturity and the pollen cones are deciduous, it is next to impossible to collect attached mature fertile material. Fallen cone scales and pollen cones abound below mature trees and should be collected.

KEY TO THE GENERA

1. Seed coat fused with cone-scale complex, apex of fertile scale forming a 'ligule', bract usually with membranous wings. Leaves spirally placed, crowded and broadly attached, variable in form from broad to scales and needles, amphistomatic . . . . **1. Araucaria**
1. Seed coat independent and extended into a wing, scale completely fused with bract which is thin but not wing-like. Leaves opposite decussate, dispersed, and narrowed to a basal petiole, broad and more or less oval, hypostomatic . . . . **2. Agathis**

1. ARAUCARIA

JUSS. Gen. Pl. (1789) 413; RICHARD, Comm. Bot. Conif. & Cycad. (1826) 153; D.DON, Trans. Linn. Soc. 18 (1841) 163; LINK, Linnaea 15 (1841) 541; ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 184; CARR. Traité Gén. Conif. (1855) 413; Man. Pl. 4 (1857) 360; GORDON, Pinetum ed. 1 (1858) 21; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 2; PARL. in DC. Prod. 16, 2 (1868) 369; BENTH. & HOOK. Gen. Pl. 3 (1880) 423; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 67; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 317; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 145; DALLIMORE & JACKSON, Handb. Conif. (1923) 150; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 263; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 80; SILBA, Phytologia Mem. 8 (1986) 38. — *Dombeya* LAMK. Enc. Méth., Bot. 2 (1786) 301, t. 828, *non* L'HÉRIT. *nec* CAV. — *Columbea* SALISB. Trans. Linn. Soc. 8 (1807) 317. — *Colymbea* SPRENG. Syst. Veg. 4, 2 (1827) 888 (refers to SALISBURY, but 'corrects' the spelling); STEUD. Nom. Bot. ed. 2, 1 (1840) 399. — **Fig. 67, 68.**

Monoecious or sometimes (temporarily?) dioecious small to immense trees mostly with limited and very formal branching elements consisting of long sweeping primary branches in false whorls along the main trunk often turned apically upward candelabra-like, then in most species only one additional rank of branches. The first branches sooner or later deciduous and in open situations replaced by adventitious branches thus producing a variety of double-crown forms. Apex of a resting shoot a cluster of incompletely formed leaves. *Leaves* spirally placed, broadly attached, crowded, multi-veined when broad and even sometimes in the needle-shaped examples, becoming uniform in size along a branch, but sometimes quite variable in the juvenile forms, amphistomatic. *Pollen cones* subtended by a cluster of reduced, leaf-like, sterile bracts, often broadened at their bases and where the mature leaves are needle-like these bracts are at least somewhat broader and flatter. Fertile bract of the seed cone broad and often extended laterally into membranous wings, the apex provided with a prominent narrow spur above the thickened apical margin. *Seed-bearing scale* only partly fused with the associated bract, its apex a free acute scale-like 'ligule' ± reaching the base of the spur on the fertile bract. *Seed coat* fused with its scale.

Distr. Across New Guinea, coastal Queensland, New Caledonia, Norfolk Island, S. & Central Chile, and southern Brazil 19 *spp.* in two sections. Fig. 65.

Fossils. In Jurassic times there was evidently an important centre of development and distribution in the Inda–Australia–Antarctic region, from whence it subsequently spread to the Kerguelen and southern Cape Colony on one hand and to Patagonia on the other. The close of the Mesozoic era seems to have witnessed its disappearance from Peninsular India, South Africa and New Zealand. Both sections had an Eogene centre in Antarctica and southern South America, one of which survives still on both sides. The oldest find of *Araucaria* was from probably Late Triassic in N. Central India (then situated in the southern hemisphere) where it remained until the Early Cretaceous whereupon it disappeared (FLORIN, K. Svensk. Vet. Ak. Handl. III, 19, 1940, 81, map 5).

KEY TO THE SECTIONS

1. Juvenile leaves bifacially flattened, cotyledons 2, pollen cones lateral .... **1. *Sect.* Araucaria**
1. Juvenile leaves acicular, cotyledons 4, pollen cones terminal .... **2. *Sect.* Eutacta**

1. Section Araucaria

Sect. Colymbea ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 185; CARR. Traité Gén. Conif. (1855) 414; Man. Pl. 4 (1857) 360; GORDON, Pinetum ed. 1 (1858) 21; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 2; PARL. in DC. Prod. 16, 2 (1868) 370 (*'Columbea'*); EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 69; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 317; PILGER

Fig. 65. Range of the genus *Araucaria* Juss. with the number of species.

in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 263; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44 (*'Columbea'*); GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7. — *Sect. Intermedia* WHITE, J. Arn. Arb. 28 (1947) 260; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7. — *Sect. Bunya* WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44. — *Subg. Colymbea* ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 99; CARR. Traité Gén. Conif. 2 (1867) 596.

Cotyledons 2, either hypogeal or epigeal, each cotyledon apparently formed of two fused units. *Juvenile leaves* narrow but distinctly flattened, spreading, often twisted into a horizontal plane; mature leaves broad and often with an acuminate tip. *Pollen cones* lateral. *Ligule* elongated and more or less constricted above the seed; cross section of the cone scale complex narrowed to a distinct and generally elongated neck above the seed, margins of the bract with or without broad membranous lateral wings.

Distr. In E. New Guinea, coastal Queensland, S. Central Chile and S. Brazil 4 non-overlapping *spp.*, of which 1 in *Malesia*.

Ecol. Trees of moist forests mostly rising above the associated trees and often colonizing disturbed areas and protecting the regrowth into that area of other trees.

Notes. *Sect. Intermedia* was established for *Araucaria klinkii* (= *A. hunsteinii*) because it differs from the rest of *sect. Araucaria* while resembling *sect. Eutacta* in epigeal cotyledons and broad membranous wings on the cone scales, but it does have two cotyledons and the spreading flat juvenile leaves of *sect. Araucaria*. One could also add that mature leaves have the hooked tip seen elsewhere only on some species of *sect. Eutacta* but the apex of the cone scale complex and the laterally placed pollen cones conform to *sect. Araucaria*. Young plants of *A. hunsteinii* are indistinguishable from those of *A. bidwillii*. *Sect. Bunya* was established for *A. bidwillii* because the cone scale complex has thick woody wings as opposed to no wings in the two American species and because of the double vascular supply to the bract and scale. The mature seed also separates from the scale complex. STOCKEY (Canad. J. Bot. 59, 1981, 1932) argues for the usefulness of these monotypic sections based on a variety of fossil material, but the differences with the residual *sect. Araucaria* hardly seems sufficiently important.

1. Araucaria hunsteinii K.SCH. Fl. Kaiser Wilhelms Land (1889) 11, t. 4, f. 8; WARB. Monsunia 1 (1900) 187, t. 10, f. B; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 324, f. 9; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 158; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) t. 2, f. 10; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 16, f. 536; HOWCROFT, For. Genet. Res. Inf. *n.* 8, FAO For. Occ. Pap. 1987/2 (1987) 31; SILBA, Phytologia Mem. 8 (1986) 41. — *A. schumanniana* WARB. Monsunia 1 (1900) 187, t. 10, f. A; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) t. 2, f. 11; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 15, f. 535. — *A. klinkii* LAUT. Bot. Jahrb. 50 (1914) 48, f. 1; LANE-POOLE, For. Res. Terr. Papua New Guinea (1925) 72; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) t. 2, f. 7; t. 3; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 15, f. 534 left.

Forest emergent 50–89 m tall with a clear bole of 35–60 m and up to 2 m diam. Branches in loose false whorls of 5 or 6 and sometimes rising towards their apex where the leaf-bearing shoots are clustered, forming a rounded crown on the upper part of the tree. In open sites after the first branches are shed a second set of smaller adventitious branches develop on the middle part of the bole. Outer bark reddish brown, rough, peeling in horizontal strips leaving a thick dark red corky flaky underbark which weathers to shades of brown. Much colourless resin is produced. Two *cotyledons c.* 35 by 1.5–2.5 mm at the base, tapering gradually to the narrow blunt apex, flat, their surface similar to the shorter broader acute first leaves which contain half a dozen parallel vascular strands evenly spaced, while the vascular strands of the cotyledons are separated into two groups by a slight gap along the centre. *Juvenile leaves* linear-ovate, narrowed to a decurrent base and tapering to a slightly acuminate pungent apex, very variable in size, less than 2 by 1 mm during resting phases to at least 2.5 by 0.5 cm in the first flush of growth and becoming larger and more lanceolate as the plant matures, twisting sharply at the base to attain a horizontal position. *Adult leaves* produced in full sunlight, often in five distinct rows, narrowed slightly at the base to a broad decurrent portion 10–15 mm long, ovate-lanceolate, nearly uniform along all but the ends of the branch, 7–15 by 1.2–2 cm, an asymmetrical dorsal ridge prolonged from the junction of the two subtending leaves, ventrally concave, inflexed at the narrow acute apex. *Pollen cones* clustering near the ends of foliage branches each in the axil of a leaf, subtended by a cluster of reduced leaves the first few more or less decussate and up to 25 mm long but not always remaining attached when the cone falls, the mature cone linear, 16–22 by 1.8–2.5 cm. *Microsporophyll* on a *c.* 4 mm peduncle, the apical part 5–10 by 2–2.5 mm and more or less linear but narrowing to an acute apex, slightly keeled on the dorsal side, margins membranous and somewhat serrate, expanded at the base on the other side of the peduncle to accommodate about 10 pollen sacs. *Seed cones* terminal on robust short branches, subtended by numerous reduced leaves, the immature cone ovoid with only the numerous lanceolate spurs visible, mature seed cones obovoid to cylindrical with the apex conical to slightly depressed, 18–25 by 12.5–16 cm, the exposed slightly expanded outer edge of each seed scale complex more or less rhomboidal in outline, the included seed 3–4 by 0.8–1 cm imbedded in the complex with the ligule extending another 2 cm but no wider than the seed and tapering at first only slightly and then more so near the acute free apex, the thick part of the fertile bract sharply expanded above the seed to its widest and thickest part at the level of the free tip of the ligule and then forming a blunt rhomboidal end or apophysis that is visible on the surface of the mature cone and includes a narrow lateral ridge on each side and terminates in a spur 9–15 mm long which is often broken off before the cone reaches maturity, the two edges of the cone bract expanded into broad blunt membranous wings each as much as 4 cm wide.

Distr. *Malesia*: E. New Guinea, in several large stands in large valleys and numerous small stands which are often clustered and with higher mountain areas intervening between the regions of occurrence (B.GRAY, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 66.

Fig. 66. Range of *Araucaria hunsteinii* K.SCH.

Ecol. Emergent in the submontane oak forest on well drained sites over a variety of soils from 520 to 2100 m. This is the tallest tree of Malesia. There has been much speculation concerning the origin of the disjunct gregarious stands. Natural regeneration does occur under forest conditions, but most vigorous germination is associated with open disturbed conditions and it is generally believed that prehistoric disturbance played a major role in producing the current distribution. Heavy commercial exploitation, pressure on regeneration by feral pigs, and anthropogenic fires have all caused serious reductions in many stands.

Uses. The basis of a major plywood industry at Bulolo which results from the fine quality of the wood and the impressive log sizes. The firm, light wood is easily worked and is yellowish brown in colour with attractive purplish streaks in the heartwood.

Vern. *Pa'a*, Watut-Bulolo, *pai*, Waria-Kaisinik, *gerau*, Waria, *bimu*, Toma, *yanguman*, Agaun, *yomejo*, Kotte-Pindui, *karina*, Bembi-Madang, *rassu*, Ongoruna, *nd'uk*, Wareng, *kembaga*, *saa'vara*, Taiora, *sowes*, Erave, Mt Matmuri.

Note. HOWCROFT (*l.c.*: 5, 31) has distinguished a glaucous variety that corresponds to *A. klinkii*. Not only are fresh leaves glaucous, but the cones are also gray-blue due to a white exudate on their surface.

2. Section Eutacta

ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 186; CARR. Traité Gén. Conif. (1855) 418; Man. Pl. 4 (1857) 361; GORDON, Pinetum ed. 1 (1858) 26; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 9; PARL. in DC. Prod. 16, 2 (1868) 372; EICHLER, in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 69; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 318; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 157; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 265; FRANCO, Port. Acta Biol. Sist. ser. B, Julio Henriques (1949) 24; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 43; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 81. — *Sect. Eutassa* (SALISB.) BENTH. & HOOK. Gen. Pl. 3 (1800) 437. — *Eutassa* SALISB. Trans. Linn. Soc. 8 (1807) 316. — *Eutacta* LINK, Linnaea 15 (1841) 543 (refers to SALISBURY, but 'corrects' the usage). — *Subg. Eutacta* (LINK) ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 99; CARR. Traité Gén. Conif. ed. 2 (1867) 604.

Cotyledons 4, epigeal. The first leaves following the cotyledons small elongated triangular scales with juvenile leaves appearing on lateral shoots or much later on the leader. *Juvenile leaves* acicular, four angled in cross section, straight or falcate and never twisted into a horizontal plane. *Adult leaves* acicular (to broad and concave towards the ventral side and with an asymmetrical dorsal ridge prolonged from the junction of the two subtending leaves), never with an acuminate tip. *Pollen cones* terminal. *Ligule* narrowing abruptly above the seed generally without any constriction; the thickened apex of the bract (apophysis) directly above the apex of the seed; margins of the bract with broad membranous lateral wings.

Distr. NE. coastal Australia (1 *sp.*), New Guinea (1 *var.*), Norfolk Island (1 *sp.*), New Caledonia (incl. Loyalty Is.) (13 *spp.*); in *Malesia* only the one variety in New Guinea.

2. Araucaria cunninghamii AIT. *ex* D.DON in Lamb. Pinus ed. 2, 3 (1837) t. 79; SWEET, Hort. Brit. 2 (1830) 475, *nomen*; LAMB. Pinus ed. 3 (1832) no pages, *nomen*; LOUD. Arb. & Fruct. Brit. 4 (1838) 2443, t. 2303–2305 *et suppl.* 2603, f. 2545; FORBES, Pin. Wob. (1839) 157, t. 52; ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 102, t. 43 & 44; ENDL. Syn. Conif. (1847) 187; CARR. Traité Gén. Conif. (1855) 419; Man. Pl. 4 (1857) 361; GORDON, Pinetum ed. 1 (1858) 27; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 9; PARL. in DC. Prod. 16, 2 (1868) 372; SIEBOLD, Flor. Jap. 2 (1870) t. 139; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 325, f. 8c; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 167; WHITE, J. Arn. Arb. 10 (1929) 200; *ibid.* 28 (1947) 259; FRANCO, Bot. Soc. Brot. 2, 23 (1949) 162; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 32; REILLY, Dept. For. Qld. Res. Pap.

Fig. 67. *Araucaria cunninghamii* AIT. *ex* D.DON *var. papuana* LAUT. in West New Guinea, Kebar Valley, Vogelkop Peninsula, 600 m alt. (Photogr. J.F.U.ZIECK, 1954).

n. 4 (1974); SILBA, Phytologia Mem. 8 (1986) 40. — *Eutacta cunninghamii* (AIT.) LINK, Linnaea 15 (1841) 543; CARR. Traité Gén. Conif. ed. 2 (1867) 608. — *Eutassa cunninghamii* SPACH, Hist. Nat. Veg. Phan. 11 (1842) 362. — **Fig. 67, 69.**

Forest emergent, 30–60 m tall, with a clear bole of 20–40 m and up to 2 m diam. Major branches tend to be in false whorls and tend to be rather straight, growing upwards at a slight angle but gradually declining with weight, persisting in open growth situations. Subsequent ramification more complex and denser than in any other *Araucaria* giving the tree the appearance of a cypress when young and a spruce when older. Outer bark at first in nearly smooth horizontal peeling strips or hoops which become smaller and rough with maturity, red in the interior but weathering to dark brown or black. There is a thick white resinous exudate. *Cotyledons* linear, *c.* 2 cm by 1.5–1.8 mm, narrowing to an acute apex, with several evenly spaced vascular strands. *Juvenile leaves* straight, linear-lanceolate, pungent, bilaterally flattened but laterally keeled, briefly decurrent forming a sharp rib on the stem, quite variable in size being tiny at the base of a shoot, most often *c.* 1 by 0.1 cm, on vigorous shoots up to 2.5 by 25 cm; leaves on the leader, particularly at the seedling stage, reduced to triangular spreading bifacially flattened scales *c.* 2 mm long. *Leaves* on older plants gradually becoming falcately curved forward and acicular. *Adult leaves* crowded and curved so that their sharply pointed apices are directed slightly inward, four-angled but about twice as wide as thick, the ultimate leafy branches *c.* 5 mm in diameter with lanceolate leaves *c.* 5 by 1.5 mm; vigorous branches at least 1 cm in diameter with leaves 7–9 by 2 mm. *Pollen cones* terminal on foliage shoots, sometimes rather short shoots, subtended by a cluster of numerous leaf-like bracts about the same size as the leaves but distinctly thinner and more crowded, the cone 4–8 cm long and 8–10 mm in diameter, linear but tapering slightly to a more or less blunt apex, formed of numerous microsporophylls. Each *microsporophyll* on a stalk 2–3 mm long, the apex extended into a triangular flat apical part 1.2–1.8 mm long, slightly keeled on the dorsal side, margins narrow and slightly serrate, with five or more pendant pollen sacs along the base. *Seed cones* terminal on robust shoots with a more or less abrupt transition to the fertile scales whose apical spines are like the leaves but bent backward, the mature spine-covered cones ovoid shaped, 6–10 by 5–7 cm. The cone scales complex less the spine 23–29 mm long and including the membranous wings *c.* 34 mm wide, the thickened end or apophysis up to 24 mm wide with a tetragonal central part *c.* 5 mm thick and bearing a strong central ridge, from the upper part of the seed to the apophysis the thickened scale extended laterally by firm lobes; a ligule covering the seed, 7–9 mm wide, narrowing sharply above the seed apex and then elongated into a triangular free apex *c.* 2 mm long and touching the edge of the apophysis; membranous wings bluntly rounded and *c.* 12 mm wide; seed completely imbedded between the scale and the ligule but indicated by an almond-shaped bulge 2 by 0.7 cm and tapering towards the micropyle at the base of the cone scale.

Distr. There are two varieties, the type in Australia and the other in New Guinea.

var. **papuana** LAUT. Bot. Jahrb. 50 (1913) 51; SILBA, Phytologia Mem. 8 (1986) 40. — *A. beccarii* WARB. Monsunia 1 (1900) 187; GIBBS, Arfak (1917) 83, f. 5. — *A. cunninghamii auct. non* AIT.: BECC. Malesia 1 (1877) 180; F.v.M. Vict. Nat. 4 (1887) 121; Descr. Not. 9 (2) (1890) 65; LANE-POOLE, For. Res. (1925) 73; HOWCROFT, For. Genet. Res. Inf. *n.* 8, FAO For. Occ. Pap. 1979/1 (1979) 9. — **Fig. 67, 69.**

Bark, particularly of younger plants, dark plum to red-brown, weathering on older plants to gray or blackish. *Juvenile leaves* up to 23–27 mm long, even on ultimate branches, contrasting sharply with Australian material: where planted side by side the Australian seedlings have leaves no more than half as long. Generally reported to be slightly bigger and more vigorous (trees 50–70 m, pollen cone 9–10 cm long, seed cone 7–12 by 6–8 cm). *Pollen cones* produced in the middle part of the mature tree and *seed cones* in the upper part.

Distr. *Malesia*: New Guinea, scattered in isolated to extensive stands from one end of the island to the other, both in the central range and along the north coast, including Japen and Ferguson Is. (B.GRAY, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 68.

Fig. 68. Range of *Araucaria cunninghamii* AIT. *ex* D.DON *var. papuana* LAUT.

Ecol. Emergent in rain-forests from 60–2745 m in a variety of rain-forest soils usually along ridges, but occasionally in swampy conditions, most often in the submontane oak forest. The higher elevation occurrences are in the more southerly part of New Guinea. Vigorous regeneration has been noticed in abandoned gardens and on old burn sites confirming that *A. cunninghamii* is a pioneer tree and a nurse for the invasion of rain-forest. On the other hand lumbering, fire, pigs, and agriculture all contribute to the destruction of natural stands.

Uses. The same as for *A. hunsteinii*, with which it often grows. The heartwood is difficult to distinguish from the sapwood.

Vern. *Pien*, Pidgin, *ungwa*, Kapauku, *sumgwa*, Manikiong, *alloa*, Marconi R., *kiriwi*, Wandammen, *ningwik*, Tambuni Valley, *makut*, Pikpik, *domooimerr, tororomooi*, Dajo, *jarujosuwa*, Tanahmerah, *flabbito*, Wapi, *d'li*, Telefomin, *escera*, Foie, *sari*, Bembi, *bontuan*, Kaigorin, *wariri*, Gurumbu, *nimola*, Esa'ala.

Note. HOWCROFT (*l.c.*) has noted in some areas of New Guinea trees that have more gracile foliage, particularly in the juvenile stage. These differences could well correspond to the type variety which therefore might include New Guinea within its range. While noting that there are slight differences, recent authors have chosen not to use the variety in describing New Guinea material perhaps because in its original description the distinctions actually given are not valid.

Fig. 69. *Araucaria cunninghamii* AIT. *ex* D.DON *var. papuana* LAUT. Tree, 49 m high, on slopes of Mt Cycloop above Lake Sentani in West New Guinea, 700 m (Photogr. F.W.RAPPARD, 1956).

2. AGATHIS

SALISB. Trans. Linn. Soc. 8 (1807) 311, t. 15, *nom. cons.* (unnecessarily); RICHARD, Comm. Bot. Conif. Cycad. (1826) 83, t. 19; WARB. Monsunia 1 (1900) 182; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 310; DALLIMORE & JACKSON, Handb. Conif. (1923) 138; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 266; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 455; FRANCO, An. Inst. Sup. Agron. 18 (1951) 101; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 75; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 126; WHITM. Trop. For. Pap. 11 (1977) 3; Pl. Syst. Evol. 135 (1980) 46, f. 1–5; SILBA, Phytologia Mem. 8 (1986) 31. — *Dammara* LINK, Enum. Hort. Berol. Alt. 2 (1822) 411, given in synonymy with *Agathis* [*non* GAERTN. Fruct. Sem. Pl. 2 (1790) 100, t. 103, f. 1, *Burseraceae*]; ENDL. Syn. Conif. (1847) 188; BLUME, Rumphia 3 (1847) 211; CARR. Traité Gén. Conif. (1855) 424; Man. Pl. 4 (1857) 363; GORDON, Pinetum ed. 1 (1858) 77; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 209; PARL. in DC. Prod. 16, 2 (1868) 374. — **Fig. 70–85.**

Monoecious trees often of immense size with clear straight boles below the globular crown, the large branches often turning irregularly upward; young trees with a conical shape. Bark at first quite smooth and light gray to reddish brown, peeling with large thin irregular flakes that gradually become thicker leaving a pitted somewhat rough reddish brown surface on larger trees. The two *cotyledons* are broad and lanceolate with an acute apex, the several vascular strands at least at first divided into two groups. Following the cotyledons the *leaves* are little more than triangular scales with a distinct central vein and several lateral veins. The first full leaves appear in pairs on lateral shoots. *Juvenile leaves* distinctly larger than adult leaves, particularly those adult leaves exposed to the sun, more or less acute, varying among the species from oval and acuminate to lanceolate. *Adult leaves* bluntly acute to rounded at the apex, rarely acuminate or lanceolate, oval to linear, sometimes lens-shaped, with considerable variation even along a single shoot where for example the first leaves may be substantially narrower than the later ones, generally somewhat reduced on seed cone bearing shoots, narrowed at the base to a brief broad petiole which is often twisted to place the leaves in a horizontal position, opposite decussate, decurrent, dispersed along the branch so that individual leaves do not overlap, with many parallel veins that converge no more than slightly towards the apex, resin canals alternating with the veins, more or less hypostomatic. Foliage buds globular, tightly covered with several pairs of overlapping scales. *Pollen cones* appearing mostly on larger trees well after the seed cones first appear, lateral and often in the axils of both of an opposite pair of leaves or occasionally terminal, subtended by several pairs of scales which form the sessile to briefly pedunculate pollen cone buds with the lowest pair sometimes expanded into reduced spreading leaves, more or less cylindrical with numerous small spirally placed microsporophylls. *Seed cone bracts* also spirally placed, their thickened

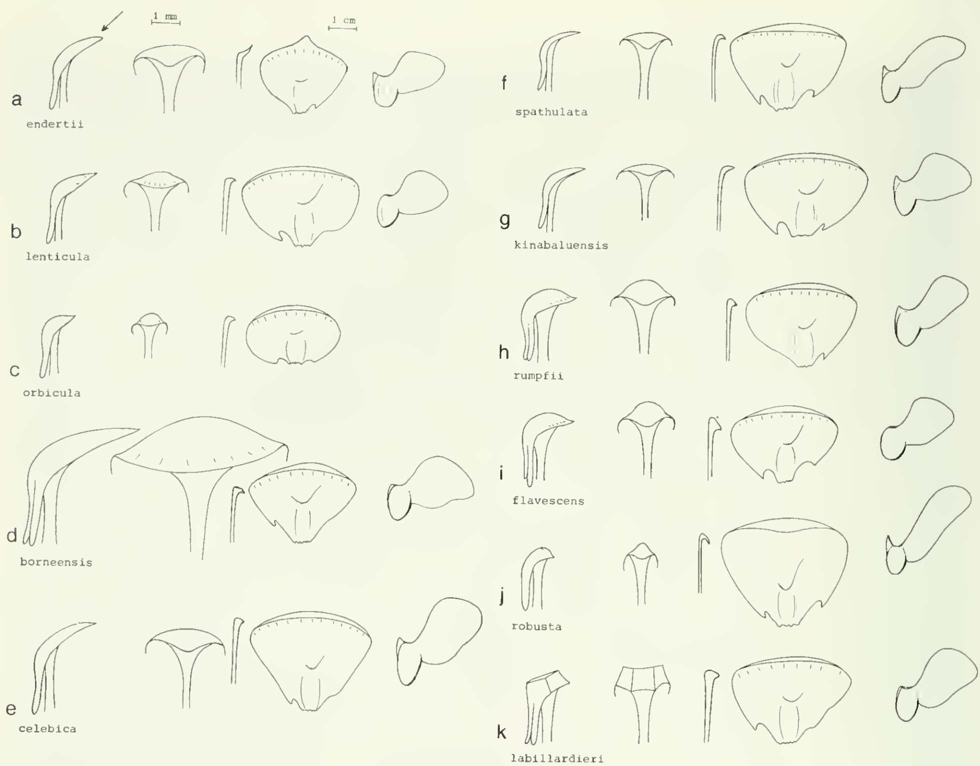

Fig. 70. *Agathis* cone elements. From left to right: lateral profile of microsporophyll, facial view of microsporophyll (from the angle indicated by arrow in the first figure), lateral profile of seed scale, facial view of seed scale (upper seed-bearing face), and seed. Microsporophylls in mm, scales and seeds in cm. — Lateral scallops of the seed scale and shape of seed wing shown are representative; these delicate structures show considerable variation. Orientation of the upper edge of the seed scale varies to which part of the cone it is in. Fully developed seed scales are formed in the middle part of the cone; numerous imperfectly formed scales occur towards the cone base and apex. Seed cone scales and seeds are laterally asymmetrical and both left-handed and right-handed cones are produced. — N.B.: under h, read *philippinensis* instead of *rumpfii.*

apical margin blunt or in some species with a projecting flattened 'beak', the lateral margins thin and broadly expanded but not membranous, normally indented near the base to form a 'scallop' which is usually much larger on one side than the other or more often one side has only a kink, quite variable especially near either end of the cone but more regular in the central fertile part, deciduous when mature. *Seed scale complex* fused with the bract. Inverted seed attached along its base, more or less flattened and oval-shaped, the margin on one side greatly expanded from the basal part into an oval membranous wing, the other margin blunt or more often with a rudimentary wing or sporadically the seed with two wings (cones and their elements come in both left and right handed versions). *Seed cone* oval to spherical.

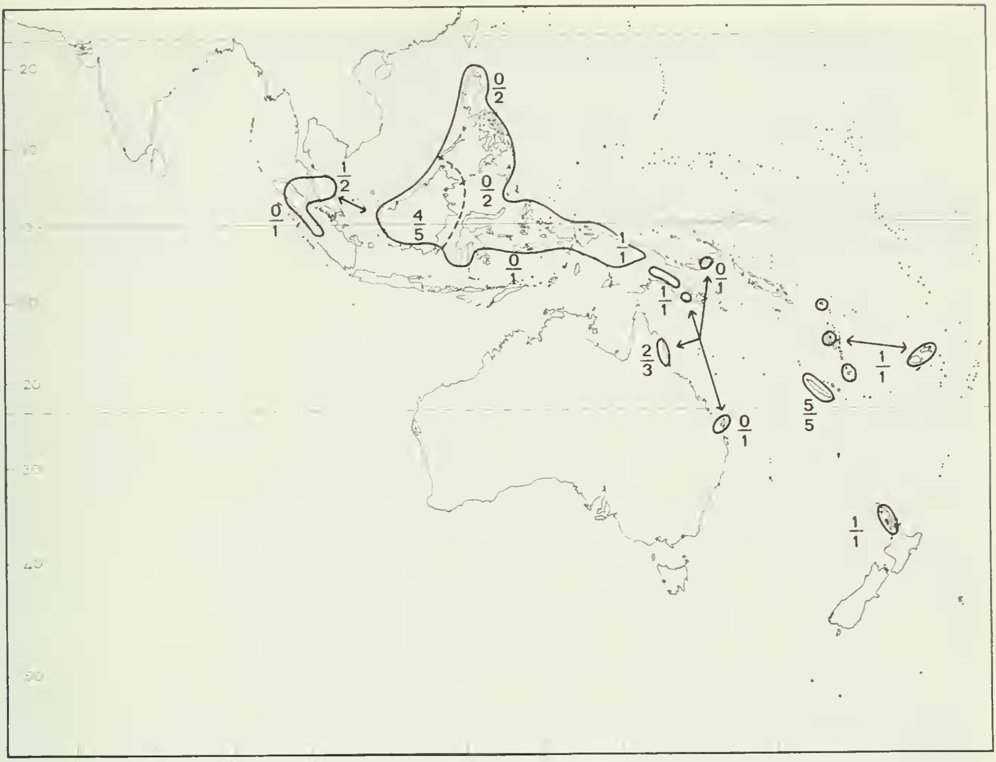

Fig. 71. Range of the genus *Agathis* SALISB. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

Distr. Three sections with 21 *spp.* from Malaya and the Philippines across New Guinea and the coast of Queensland to Fiji and northern New Zealand; in *Malesia* 11 *spp.* There is a gap in the Solomons. Fig. 71.

Fossils: Fossil wood attributed to *Agathis* has been found in the Upper Cretaceous and Tertiary of New Zealand and from the Jurassic to the Tertiary in Australia, as well as in the Tertiary of Western Australia. Cone scales have been found in the northern hemisphere but the identification is uncertain (FLORIN, K. Svenska Vet. Ak. Handl. III, 19, 1940, *n.* 2, 82; Acta Horti Berg. 20 (4), 1963, 180, f. 15 map).

Ecol. The majority belong to lowland rain-forests.

KEY TO THE SECTIONS

1. Dorsal part of the microsporophyll not at all angled.
   2. Seed scale only slightly angled to completely blunt. *Spp.* 1–8 .... 1. *Sect.* **Agathis**
   2. Seed scale with a distinct beak (seed cone small, 5–6 cm diam. by 6–7 cm long). *Sp.* 9 2. *Sect.* **Rostrata**
1. Dorsal part of the microsporophyll sharply angled. *Spp.* 10–11 .... 3. *Sect.* **Prismobracteata**

1. Section Agathis

Sect. Macrobracteatae MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 457. — *Sect. Microbracteatae* MEIJER DREES, *l.c.* 461.

Fig. 72. Flaky bole of *Agathis borneensis* WARB. in heath forest on podsolized white sandy terrace, *c.* 20 m alt., Brunei (Photogr. P.S.ASHTON, May 1959).

Large trees. *Pollen cones* with spoon-shaped microsporophylls without angled creases, rarely sessile. *Seed cones* in most cases at least 7 cm long and the seed bracts always blunt along their apical margins.

Distr. In the same territory as the genus less the more southerly areas 13 *spp.*, of which 8 in *Malesia.*

KEY TO THE SPECIES

1. Juvenile (and more accessible) leaves not at all acuminate, adult leaves at least 6 cm long or else glaucous on the underside.
2. Leaves not glaucous on the underside, at least 6 cm long. Pollen cones at least 4 cm long. Microsporophylls slightly acute and nearly as long as wide or large (over 5 mm long).
3. Pollen cone at least 2 cm in diameter. Microsporophyll *c.* 6 mm wide, over 5 mm long, and blunt, resin canals in the leaves paired . . . . **1. A. borneensis**
3. Pollen cone more than 14 mm in diameter. Microsporophyll no more than 2.5 mm wide, 2 mm long, and slightly acute, resin canals in the leaves solitary.
4. Adult leaves never broadly rounded at the apex. Pollen cones 12–14 mm in diameter. Apex of microsporophyll at least 2 mm long and wide. Seed bract at least 42 mm wide and 32 mm high with more or less straight margins and the apex bluntly ridged . . . . **2. A. celebica**
4. Adult leaves acute to broadly rounded at the apex. Pollen cones 9–12 mm in diameter. Apex of microsporophyll less than 2 mm wide and 1.5 mm long. Seed bract less than 42 mm wide and 32 mm high with more or less rounded margins and the apex sharply rigid . . . . **3. A. spathulata**
2. Leaves glaucous on the underside, no more than 6 cm long. Pollen cones less than 4 cm long. Microsporophylls blunt (much wider than long), less than 2 mm long.
5. Adult leaves lens-shaped, 5–7 cm long. Pollen cones 3–4 cm by 9–10 mm. Microsporophyll 2–2.5 mm wide. Seed cone *c.* 6 cm in diameter, spherical . . . . **4. A. lenticula**
5. Adult leaves orbicular, blunt, 2.4–4 cm long. Pollen cones 8–14 by 4–6 mm. Microsporophyll 1.2–1.5 mm wide. Seed cone *c.* 4.5 cm in diameter, elongated . . . . **5. A. orbicula**
1. Juvenile leaves distinctly acuminate. Adult leaves less than 6 cm long and not glaucous on the underside.
6. Adult leaves not acuminate. Microsporophyll helmet-shaped, the stalk attached near the centre of the apical part, at least 2 mm wide. Apex of the seed cone bract bluntly ridged.
7. Seed sharply angled opposite the wing. Mature pollen cone mostly at least 3.5 cm long by 10 mm in diameter. Seed cone bract 2.8–3.2 cm high. Adult leaves at least 4.5 cm . . . . **6. A. philippinensis**
7. Seed bluntly rounded opposite the wing. Mature pollen cone 2–3.5 cm long by 7–10 mm in diameter. Seed cone bract 2.6–2.9 cm high. Adult leaves 3–4 cm long. . . . . **7. A. flavescens**
6. Adult leaves acuminate or small and blunt. Microsporophyll shingle-shaped, the stalk attached below the centre of the apical part, 1.6–1.8 mm wide. Apex of the seed cone bract sharply ridged **8. A. kinabaluensis**

1. Agathis borneensis WARB. Monsunia 1 (1900) 184, t. 80; DALLIMORE & JACKSON, Handb. Conif. (1923) 143; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 459; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 96, t. 573; DE LAUB. Blumea 25 (1979) 532, t. 1; WHITM. Pl. Syst. Evol. 135 (1980) 54, t. 1 f. 3, t. 2. f. 3, t. 4; VELDKAMP & DE LAUB. Taxon 33 (1984) 345; SILBA, Phytologia Mem. 8 (1986) 32. — *Pinus dammara* LAMB. Descr. Pinus 1 (1803) 61, t. 38 (& 38a), *nom. rej.*; VELDKAMP & DE LAUB. Taxon 33 (1984) 337. — *A. loranthifolia* SALISB. Trans. Linn. Soc. Lond. 8 (1807) 312, t. 15, *nom. superfl.* — *Dammara loranthifolia* (SALISB.) LINK, Enum. Hort. Berol. Alt. 2 (1822) 411. — *Dammara orientalis* LAMB. Descr. Pinus 2 (1824) 15, *nom. superfl.*; GORDON, Pinetum ed. 1 (1858) 79. — *A. dammara* (LAMB.) RICHARD, Comm. Bot. Conif. & Cycad. (1826) 83, t. 19. — *Abies dammara* (LAMB.) DESF. Tabl. Ecol. Bot. ed. 3 (1829) 356. — *Dammara orientalis var. orientalis* CARR. Traité Gén. Conif. (1855) 426; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 210. — *A. beccarii* WARB. Monsunia 1 (1900) 184, t. 8F; DALLIMORE & JACKSON, Handb. Conif. (1923) 142; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 458, f. 1. — *A. macrostachys* WARB. Monsunia 1 (1900) 183, t. 8A. — *A. rhomboidales* WARB. *l.c.* 184, t. 8C; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 460; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 103. — *A. alba* FOXW. Philip. J. Sc. 4 (1909) Bot. 442. — *A. latifolia* MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 459. — *A. dammara ssp. dammara* WHITM. Pl. Syst. Evol. 135 (1980) 56 (WHITMORE described *A. celebica* and *A. philippinensis*). — **Fig. 72, 73.**

Huge tree to 55 m tall. *Juvenile leaves* ovate-lanceolate, up to 14 by 4 cm. *Adult leaves* ovate with

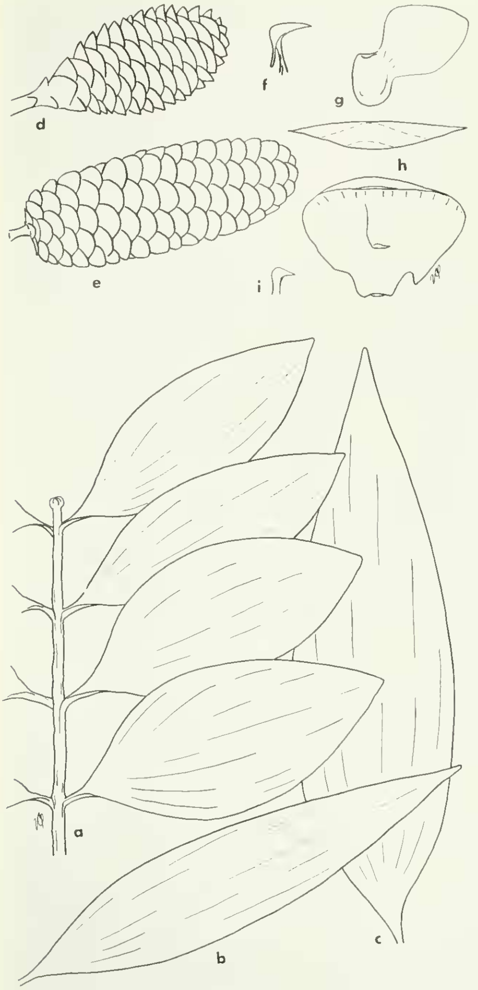

Fig. 73. *Agathis borneensis* WARB. a. Mature foliage shoot; b. leaf variation of shaded branches or alternating with a; c. juvenile leaf; d. young seed cone; e. mature pollen cone, all ×0.4; f. profile view of microsporophyll, ×1.25; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

a more or less acute apex, 6–12 cm by 20–35 mm, tapering at the base to a *c.* 5 mm petiole. The most common foliage leaf *c.* 7 by 3 cm but branches with relatively long and narrow leaves often interspersed with the more usual type and more general on younger trees. Resin ducts in pairs one above the other between most vascular strands rather than the prevailing solitary duct elsewhere in the genus. *Mature pollen cones* oblong, 4–7 cm by 20–25 mm, rounded at the apex, subtended by a 2–10 mm peduncle, the apex of the microsporophyll spoon-shaped, 5.5–6.5 by 4–5 mm, the apex a broad semicircle. *Mature seed cones* oval, 6–8.5 by 5.5–6.5 cm. *Seed bract* roughly triangular but well rounded at the upper corners, a low thick ridge along the apical margin, a strongly hooked 6 mm scallop on one side of the base, the other side with no more than a kink, 26–28 by 36–40 mm. *Seed c.* 12 by 9 mm, blunt at one upper corner and a broadly rounded wing *c.* 20 by 16 mm at the other corner.

Distr. *Malesia*: throughout Borneo and more restricted areas in Malaya and N. Sumatra. Fig. 74.

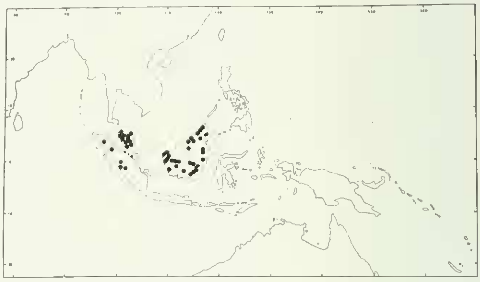

Fig. 74. Range of *Agathis borneensis* WARB.

Ecol. Scattered in upland rain-forest from low elevations to 1200 m throughout its range and in dense nearly pure stands on low-lying sandy peat soil in many parts of Borneo and in one area in Malaya. It is of interest to note that *Dacrydium pectinatum* has a similar ecology.

Vern. Malaya: *dammar, dammar daging, dammar minyak, tulong*, M; Sumatra: *hedje*, Tapanuli; Borneo: *bindang*, Sarawak, *bulu*, Iban, *salang*, Kedayah, *tambunan*, Sabah, *manggilam*, Dusun, *bangalan, bengalan*, Sampit, Pilau, *toga*, W. Kutai, *bembuëng*, SE. Borneo, *nuju*, Dajak, *enghatan*, Sanggan, *pisau, putut*, Sintang.

Note. If the proposal to reject *Pinus dammara* LAMB. in favour of *Agathis borneensis* WARB. is not accepted, the proper name of this species would be *Agathis dammara* (LAMB.) RICHARD, a name heretofore (incorrectly) associated with different species of Celebes, the Moluccas and the Philippines (see under *A. celebica* and *A. philippinensis*). If various closely related species were combined as varieties or subspecies under this species, there would be no reason to reject the name *Agathis dammara*.

2. Agathis celebica (KOORD.) WARB. Monsunia 1 (1900) 185; DALLIMORE & JACKSON, Handb. Conif.

(1923) 143; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 461; DE LAUB. Kalikasan 7 (1978) 146; Blumea 24 (1978) 504, f. 2; SILBA, Phytologia Mem. 8 (1986) 32. — *Dammara alba* RUMPH. *ex* HASSK. Tijd. Nat. Gesch. Phys. 9 (1842) 179; PARL. in DC. Prod. 16, 2 (1868) 374. — *Dammara rumphii* PRESL, Epim. Bot. (1851) 236, *nom. superfl.* — *Dammara orientalis var. pallens* CARR. Traité Gén. Conif. (1855) 426. — *Dammara orientalis var. alba* KNIGHT *ex* HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 211. — *Dammara alba var. alba* HASSK. Abh. Naturf. Ges. Halle 9 (1866) 180. — *Dammara alba var. celebica* HASSK. *l.c.* — *Dammara celebica* KOORD. Meded. Lands Pl. Tuin 19 (1898) 263. — *A. dammara auct. non* RICHARD: WARB. Monsunia 1 (1900) 182, t. 9, f. 1; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 98; DE LAUB. Blumea 24 (1978) 503, f. 1. — *A. alba auct. non* FOXW.: MERR. Rumph. Herb. Amb. (1917) 76; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 466; DALLIMORE & JACKSON, Handb. Conif. ed. 3 (1948) 178. — *A. beckingii* MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 463. — *A. hamii* MEIJER DREES, *l.c.* 462, f. 1. — *A. loranthifolia auct. non* SALISB.: MEIJER DREES, *l.c.* 464. — *A. celebica ssp. celebica* VELDKAMP & WHITM. in Veldkamp & De Laub. Taxon 33 (1984) 345. — *A. dammara ssp. dammara auct. non* WHITM.: WHITM. Pl. Syst. Evol. 135 (1980) 57, *p.p.*

Huge tree to 65 m tall. *Juvenile leaves* ovate-lanceolate, up to 15 by 4.6 cm. Shade leaves on mature trees acute and roughly 9 by 3 cm. *Leaves* from fully exposed branches well rounded at the apex but still tapering, not blunt, 6–8 by 2–3 cm, tapering at the base to a 5–10 mm petiole. *Pollen cones* after shedding pollen 4–6 by 1.2–1.4 cm or possibly even larger, subtended by a short peduncle *c.* 3 mm long, normally axillary but sometimes terminal (*A. beckingii*). The apical part of the *microsporophyll* spoon-shaped, spreading, with the stalk attached well behind its centre, *c.* 2.5 mm by 2 mm and slightly angled at the apex. *Seed cone* oval, 9–10.5 by 7.5–9.5 cm. *Seed bract* with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its lateral margins, roughly triangular in shape, the lateral margins nearly straight with a small scallop 4–8 mm above the base on one side, the upper corners more or less angular and rigid, 32–36 by 42–45 mm. *Seed c.* 14 by 9 mm with a short acute projection on one upper corner and a broad rounded wing *c.* 24 by 16 mm at the other.

Distr. *Malesia*: Celebes and Moluccas to Palawan in the Philippines and probably other parts of southern Philippines. Fig. 75.

Ecol. A forest emergent scattered and locally common in lowland rain-forest from near sea-level to 1200 m.

Fig. 75. Range of *Agathis celebica* (KOORD.) WARB.

Vern. *Dammar, dammar radja*, M, *hulontuu*, Malili, *kawo*, Maliki, *kisi*, Buru, *salo*, Ternate, *dayungon*, Samar, Philippines.

Note. WHITMORE (1980) insists that he can find no difference between this and *A. philippinensis* among others and certainly the vast majority of the collected materials (shade leaves and immature reproductive organs) is enigmatic. WHITMORE's descriptions show he is dealing with immature material and the notion that pollen cones continue growth after shedding their pollen is inadmissible. Groups of both species grow side by side at Bogor, where properly mature material can be compared and sharp differences easily seen. Because this is the only species known on Ambon, it is the species which RUMPHIUS (Herb. Amb. 2, 1741, 174, t. 57) has in mind and, like the closely related *A. borneensis*, which occupies similar habitats west of the Makassar Strait, is an important producer of the resin known as dammar.

3. Agathis spathulata DE LAUB., *sp. nov.*; SILBA, Phytologia Mem. 8 (1986) 37, *nom. inval.* — *A.*

robusta ssp. nesophila WHITM. Pl. Syst. Evol. 135 (1980) 64.

Arbor magna ad 60 m alta. Folia adulta acuta 9–10 cm × 20–30 mm ad spathulata 7–9 cm × 18–20 mm. Strobili masculini 9–13 mm diametri, 4–7 cm longi, apicis microsporophyllis 1,5–2 mm latis, 1,3–1,5 mm longis. Squamae femineae 35–42 mm latae, 27–32 mm altae, marginibus rotundibus apicis costis acutis. Holotypus: DE LAUBENFELS P741 (L).

Huge tree to 60 m tall. *Juvenile leaves* ovate-lanceolate, not at all acuminate, up to 13 by 4.5 cm. *Adult leaves* bluntly acute, 9–10 cm by 20–30 mm to broadly rounded and 7–9 cm by 18–20 mm, tapering at the base to a 5–10 mm petiole. *Mature pollen cones* 4–7 cm by 9–13 mm, subtended by a 2–9 mm peduncle, the apex of the microsporophyll spoon-shaped without ridges, 1.5–2 by 1.3–1.5 mm, broadly acute. *Seed cone* oval, 8.5–10 by 6.5–7.5 cm. *Seed bract* with a thin sharp ridge along the apical margin, broadly rounded at the upper corners, a small 6 mm scallop on one side of the base and a larger 10 mm scallop on the other, 27–32 mm high by 35–42 mm broad. *Seed c.* 10 by 6 mm, with a sharp projection on one upper corner and an elongated bent wing *c.* 24 by 10 mm at its widest at the other corner.

Distr. *Malesia*: SE. New Guinea, E. Highland, near Obura. Fig. 76.

Fig. 76. Range of *Agathis spathulata* DE LAUB. (squares) and *A. labillardieri* WARB. (dots).

Ecol. Scattered as a rain-forest emergent or surviving in small exposed groves between 900 and 1980 m.

Vern. *Asong, muwaka, ogapa.*

Note. The seed cone scale and seed, though smaller, resemble those of *A. robusta*, a lowland species, but the pollen cone in particular is quite different.

4. Agathis lenticula DE LAUB. Blumea 25 (1979) 537, f. 4; SILBA, Phytologia Mem. 8 (1986) 34. — **Fig. 77.**

Large tree to 45 m tall. *Juvenile leaves* to 11 cm by 47 mm, ovate, tapering to an acute, scarcely acuminate apex and more sharply at the base. *Adult leaves* lens-shaped, more or less acute, 5–7 cm by 18–24 mm, tapering to a 3–7 mm petiole, glaucous on the underside. *Mature pollen cones* 3–4 cm by 9–10 mm, subtended by a 2–6 mm peduncle, the apex of the microsporophyll spoon-shaped and spreading, 2–2.5 by 1.5–2 mm, apex blunt. *Seed cone* nearly spherical, *c.* 7 by 6 cm. *Seed bract* with a thin sharp ridge along the apical margin, lateral margins broadly rounded with a strongly hooked scallop 7 mm above the base on one side, *c.* 27 mm high by 38–45 mm broad. *Seed c.* 11 by 7 mm with a slight blunt to no projection on one upper corner and a broadly rounded wing *c.* 8 by 14 mm at the other corner.

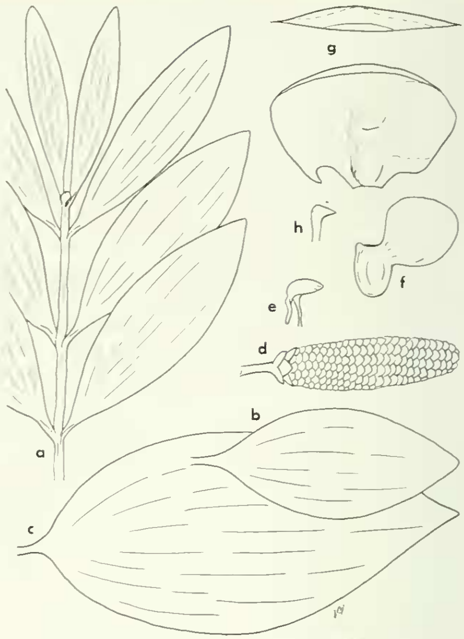

Fig. 77. *Agathis lenticula* DE LAUB. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone, all ×0.4; e. profile view of microsporophyll, × 1.25; f. seed; g. end view and facial view of the seed cone scale; h. profile view of the upper edge of the same.

Distr. *Malesia*: Sabah (Mt Kinabalu and the Crocker Range). Fig. 78.

Ecol. Emergent in mountain rain-forest, 1140–1680 m.

Vern. *Tanggilan, tengilan, tungilan*, Dusun.

Note. This species occurs just below *A. kinabaluensis* on Mt Kinabalu where the two can easily be compared in the field. The distinctive leaf shapes are readily apparent but in herbarium specimens the

Fig. 78. Range of *Agathis lenticula* DE LAUB. (circles) and *A. orbicula* DE LAUB. (dots).

glaucous leaf undersurface is generally not detectable. Other differences are the larger pollen cones with blunt, not angled, microsporophylls and the lack of a sharp projection at the upper corner of the seed. Besides *A. orbicula* and *A. endertii*, other *Agathis* species with glaucous leaf undersides occur far to the east beyond Malesia.

5. **Agathis orbicula** DE LAUB. Blumea 25 (1979) 540, f. 5; SILBA, Phytologia Mem. 8 (1986) 36. — **Fig. 79.**

Tree to 40 m tall. A light yellow resin is produced in some abundance. *Juvenile leaves* ovate and bluntly acute, to 6.5 cm by 28 mm. *Adult leaves* ovate to orbicular, broadly rounded to slightly angled at the apex, 24–40 by 12–24 mm, tapering sharply at the base to a 3–7 mm petiole, glaucous on the underside. *Mature pollen cones* 8–14 by 4–6 mm, subtended by a 2–6 mm peduncle, the apex of the microsporophyll helmet-shaped, 1.2–1.5 by 1–1.2 mm, apex blunt. *Seed cone* oval, *c.* 7 by 4.5 cm. *Seed bract* with an acute ridge along the apical margin, ovate with a 4 mm scallop spreading nearly perpendicularly to each side of the base, *c.* 20 mm high and 33 mm broad. *Seed* unknown but leaving a blunt impression suggesting a shape like that of *A. lenticula*.

Distr. *Malesia*: S. Sabah to Central Sarawak. Fig. 78.

Ecol. Scattered in rain-forests and kerangas on low mountains and plateaus between 450 and 1050 m.

Vern. *Tumuh*, Murut, *tubu*, Kenyah, *bulok*, Iban.

6. **Agathis philippinensis** WARB. Monsunia 1 (1900) 185, t. 8E; DALLIMORE & JACKSON, Handb. Conif. (1923) 147; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 468; SILBA, Phytologia Mem. 8 (1986) 36. — *Dammara rumpfii auct. non* PRESL: PRESL, Epim. Bot. (1841) 236. — *A. regia* WARB. Monsunia 1 (1900) 183, t. 8B; DALLIMORE & JACKSON, Handb. Conif. (1923) 147. — *A. alba auct. non* FOXW.: FOXW. Philip. J. Sc. 4 (1909) Bot. 442. — *A. dammara auct. non* RICHARD: DE LAUB. Kalikasan 7 (1978) 144; Blumea 24 (1979) 499, f. 1. — *A. dammara ssp. dammara auct. non* WHITM.: WHITM. Pl. Syst. Ecol. 135 (1980) 56, *p.p.*, t. 5, f. 1 & 2.

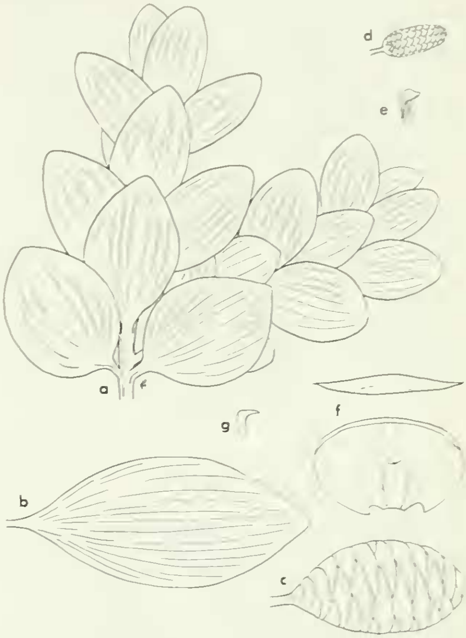

Fig. 79. *Agathis orbicula* DE LAUB. a. Mature foliage shoots; b. juvenile leaf; c. young seed cone; d. mature pollen cone, all ×0.4; e. profile view of microsporophyll, ×1.4; f. end view and facial view of the seed cone scale; g. profile view of the upper edge of the same.

Huge tree to 60 m tall. Abundant white resin produced. *Juvenile leaves* ovate and distinctly acuminate, to 7 by 3 cm. *Adult leaves* ovate, very slightly to distinctly acute, 4–6 by 1.5–2 cm, the smaller leaves, which probably derive from more exposed position, being the least acute, tapering at the base to a 5–8 mm petiole. *Mature pollen cones* 2.5–4.5 cm by 10–11 mm, subtended by a short peduncle, the apex of the microsporophyll helmet-shaped with the stalk attached close to its centre, 2–2.5 by 1.5–2 mm, the apex very slightly angled. *Seed cone* oval, 7–9 by 12 cm. *Seed bract* with a low thick ridge along apical margin, broadly rounded at the upper corners, a small 3–6 mm scallop on one side of the base, 28–32 mm high by 35–45 mm broad. *Seed c.* 11 by 6 mm, broadly acute at one upper corner and with a wing *c.* 20 by 11 mm at its widest at the other corner.

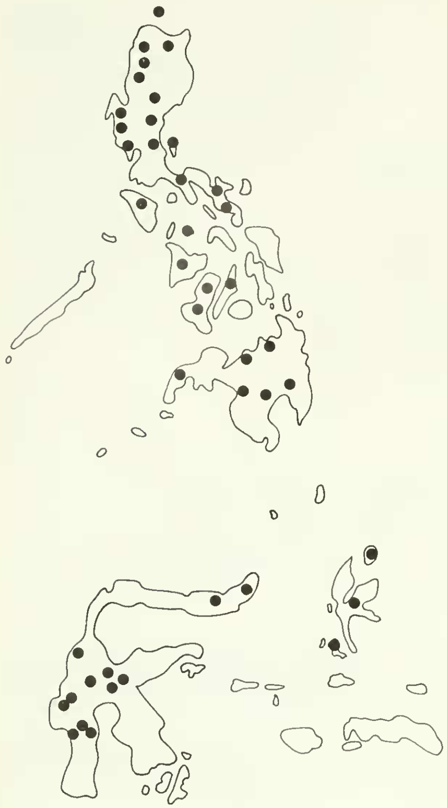

Fig. 80. Range of *Agathis philippinensis* WARB.

Distr. *Malesia*: Philippines to Celebes and Halmaheira. Fig. 80.

Ecol. Scattered and often emergent in upland rain-forest, mostly 1200–2200 m, occasionally as low as 450 m in Halmaheira, 900 m in Celebes and far to the north in Luzon to 250 m.

Vern. *Dammar*, M, *goga, solo, tjoga*, Manado, *molewaun*, Teliwang, *almaciga*, Philippines, *dayungon*, Samar, *dingan*, Misamis.

Note. Reports by foresters of 'different' trees in the southern parts of the Philippines may well apply to *A. celebica* which has been collected there. Most Philippine collections are of nondescript leaves and (rarely) immature cones.

7. Agathis flavescens RIDLEY, Kew Bull. (1914) 332; J. Fed. Mal. St. Mus. 6 (1915) 3; DALLIMORE & JACKSON, Handb. Conif. (1923) 143; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 464; SILBA, Phytologia Mem. 8 (1986) 33. — *A. dammara ssp. flavescens* (RIDLEY) WHITM. Pl. Syst. Evol. 135 (1980) 59. — *A. celebica ssp. flavescens* (RIDLEY) VELDKAMP & WHITM. *ex* VELDKAMP & DE LAUB. Taxon 33 (1984) 346.

Small to medium-sized tree to 12 m tall. *Juvenile leaves* ovate-lanceolate and slightly acuminate, up to 8 cm by 32 mm. *Adult leaves* ovate and, unlike most adult *Agathis* leaves, often wider before the middle, 3–4 cm by 10–20 mm, rounded and blunt at the apex or very slightly angled, tapering at the base to a 3–5 mm petiole. *Mature pollen cones* 20–35 by 8–9 mm, subtended by a 2–8 mm peduncle, the apex of the microsporophyll helmet-shaped, 2 by 1.8 mm, the apex slightly angled. *Seed cone* oval, 6–7 by 7–8 cm. *Seed bract* with a thick ridge along the apical margin, broadly rounded at the upper corners, a large scallop more than one cm from the base on one side and a smaller *c.* 6 mm scallop on the other, 26–29 by 35–37 mm. *Seed* oval, *c.* 11 by 9 mm, blunt at one upper corner and with a broad wing 17 by 14 mm at its widest at the other corner.

Distr. *Malesia*: the two or three highest peaks in Peninsular Malaya.

Ecol. Scattered trees above a low summit scrub, 1200–1800 m, the leaves often yellow, suggesting adaptation to difficult nutrient conditions.

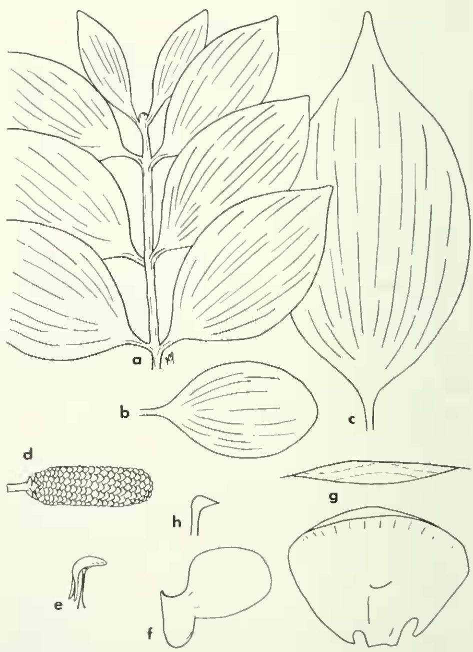

Fig. 81. *Agathis kinabaluensis* DE LAUB. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone; all ×0.4; e. profile view of microsporophyll, ×1.25; f. seed; g. end view and facial view of the seed cone scale; h. profile of the upper edge of the same.

Note. This species corresponds in Malaya to *A. philippinensis* which it strongly resembles, differing in smaller cones, somewhat differently shaped leaves and seeds and especially by the blunt corner of the seed opposite the wing.

8. Agathis kinabaluensis DE LAUB. Blumea 25 (1979) 535; SILBA, Phytologia Mem. 8 (1986) 34. — **Fig. 81.**

Small to large tree to 36 m tall. *Juvenile leaves* ovate and strongly acuminate, to 9 cm by 44 mm. *Adult leaves* ovate, slightly acuminate or occasionally on the smaller leaves round and blunt, 3.5–7 cm by 18–32 mm, tapering at the base to a 4–7 mm petiole. *Mature pollen cones* 18–30 by 8–10 mm, nearly sessile to a 4 mm peduncle at the base, the apex of the microsporophyll spoon-shaped, spreading slightly, 1.6–1.8 by 1.2–1.6 mm, the apex very slightly angled. *Seed cone* oval, 7.5–8.5 by 11 cm. *Seed bract* with a prominent narrow ridge along the apical margin, broadly rounded at the upper corners, a smaller 4 mm and a larger 6 mm scallop on either side of the base, 28–32 by 40–45 mm. *Seed c.* 11 by 7 mm, prominently acute at one upper corner and with a broad wing 20 by at least 12 mm at the other corner.

Distr. *Malesia*: Mt Kinabalu in Sabah.

Ecol. In or rising slightly above the mossy forest and rather small where the forest is stunted, 1500–2400 m.

Vern. *Tumu*, Murut.

Note. This species in Borneo corresponds in many ways with *A. philippinensis* but is nevertheless substantially different.

2. Section Rostrata DE LAUB., *sect. nov.*

Arboris. Squama feminea projectioni apici instructa. Strobilus femineus 5–6 × 6–7 cm. Strobilis masculinus sessilus. Typus: Agathis australis.

Small to large trees. *Leaves* ovate and slightly angled at the apex to round and blunt, the leaf undersides distinctly glaucous, solitary resin canals between the vascular bundles. *Juvenile leaves* more acute. *Pollen cones* more or less sessile. *Microsporophylls* spoon-shaped, more or less acute and spreading. *Seed cones* spherical to oval and rather small, 5–6 by 6–7 cm. *Seed bract* with a distinct projection or beak near the centre of the ridged apical margin. *Seeds* broadly oval with a blunt projection at one upper corner and a broad wing at the other corner.

Distr. There are 3 *spp.*, widely separated, in New Zealand (1 *sp.*), in New Caledonia (1), and in *Malesia*: Borneo (1).

Note. The projection on the seed bract corresponds to the ligule in *Araucaria* and other conifers and for *Agathis* is a primitive trait.

9. Agathis endertii MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 470; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 99; DE LAUB. Blumea 25 (1979) 534, f. 2; SILBA, Phytologia Mem. 8 (1986) 33. — **Fig. 82.**

Tree to at least 48 m. *Juvenile leaves* apparently lanceolate. *Adult leaves* ovate and broadly acute to semicircular and blunt at the apex, 5–8 cm by 17–36 mm with considerable variation on individual specimens, tapering to a 3–6 mm petiole, glaucous on the underside. *Mature pollen cones* 26–38 by 7 mm, sessile, the apex of the microsporophyll spoon-shaped, spreading, 2.5 by 2 mm, the apex slightly angled. *Seed cone* oval, 4.5 by 7 cm. *Seed bract* with a prominent narrow ridge along the apical margin surmounted by a spreading blunt more or less triangular projection *c.* 8 by 3 mm, somewhat rounded at the upper corners, a small 4 mm scallop on one side at the base, at least 25 mm by 30 mm. *Seed c.* 11 by 8 mm, a short acute projection on one upper corner, a broad wing *c.* 18 by 14 mm at its widest at the other corner.

Distr. *Malesia*: Borneo. Fig. 83.

Ecol. In more or less isolated populations from near sea-level to 1440 m, often associated with sandstone kerangas.

Vern. *Bulok*, Iban.

Note. The leaves more or less resemble in particular *A. borneensis* (but lack the paired resin canals) so that sterile specimens cannot be readily identified in this otherwise quite distinct species.

Fig. 83. Range of *Agathis endertii* MEIJER DREES.

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Fig. 82. *Agathis endertii* MEIJER DREES. a. Mature foliage shoot; b. leaf variation; c. juvenile leaf; d. young seed cone; e. mature pollen cone, all ×0.4; f. profile view of microsporophyll, ×1.25; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

3. Section Prismatobracteatae

MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 470.

Large trees. *Microsporophylls* with sharp creases dividing the apical part into three or more facies. *Pollen cones* with a short peduncle. *Seed bracts* always blunt along their apical margins. *Leaves* not glaucous underneath.

Distr. From New Guinea and New Britain to Queensland, New Caledonia and Vanuatu (New Hebrides) 5 *spp.*; in *Malesia*: 2 *spp.*

KEY TO THE SPECIES

1. Apical part of pollen cone prismatic with a series of lateral facies surrounding a flat hexagonal upper face **10. A. labillardieri**
1. Apical part of pollen cone divided into three lateral facies . . . . **11. A. robusta**

10. Agathis labillardieri WARB. Monsunia 1 (1900) 183; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 471; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 99; WHITM. Pl. Syst. Evol. 235 (1980) 60; SILBA, Phytologia Mem. 8 (1986) 34. — **Fig. 84, 85.**

Huge tree to 60 m. *Juvenile leaves* ovate and acuminate, to 10 by 6 cm. *Adult leaves* ovate to oval lanceolate, acute, 6–9 cm by 20–24 mm, narrowing to a 5–7 mm petiole. *Mature pollen cones* 25–35 by 10–15 mm, subtended by a 2–6 mm peduncle, the apical part of the microsporophyll prismatic with a series of lateral facies surrounding a flat hexagonal upper face 1–1.5 mm wide and long and crowded so that only the upper face is exposed. *Seed cone* oval, 8.5–10 by 7.5–9 cm. *Seed bract* with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its margins, roughly triangular in shape with nearly straight lateral margins, with a distinct scallop *c.* 8 mm above the base on one side, slightly rounded at the upper corners, 30–32 by 38–42 mm. *Seed c.* 12 by 7 mm with a short broadly acute projection on one upper corner and a broad rounded wing *c.* 20 by 15 mm at the other.

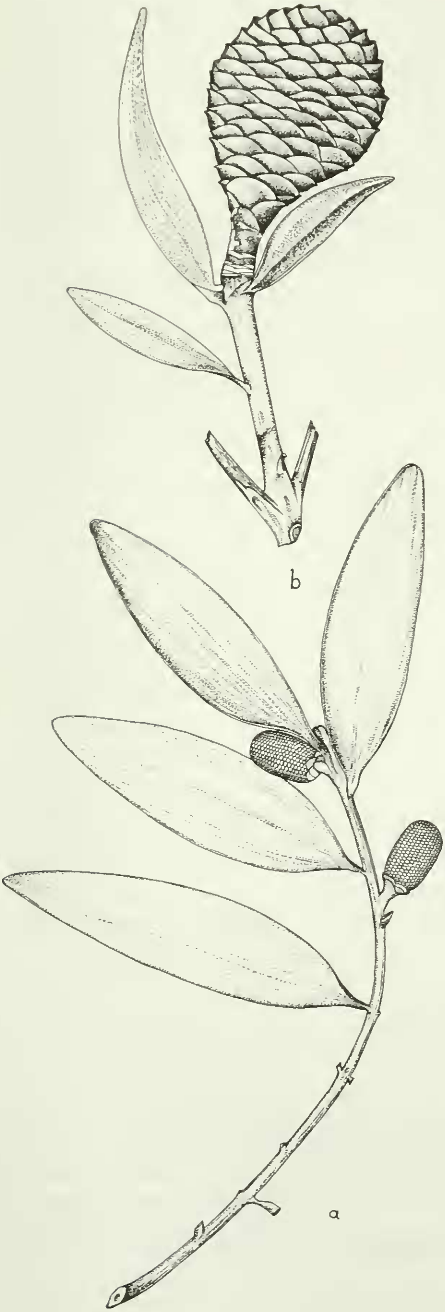

Fig. 84. *Agathis labillardieri* WARB. a. Twig with pollen cones; b. seed cone, both ×0.4.

Fig. 85. Cones of *Agathis labillardieri* WARB. of a specimen growing in Sarmi on the north coast of West New Guinea (Photogr. H.R.KARSTEL, 1957).

Distr. *Malesia*: throughout the western part of New Guinea and eastward to the margins of the Sepik Valley. Fig. 76.

Ecol. From near sea-level to 1350 m or occasionally to 1800 m, often on ultrabasic soil and locally very common.

Vern. *Dammar*, M, *pen*, Pidgin, *legatulus*, Mooi lang., *aisjier*, Arguni, *idjir*, Irahutu, *tar*, Kebar, *waiui*, Pousami, *kessi*, Roberai, Kuri, *fuko*, Manikiong, *uto*, Kapauku, *warkai*, Kamora, Kokonao, *osier*, Itik, *sao*, Kwerba, *wel*, Iwer, *nu*, Wagu, *aglo*, Orne, *koba*, E. Sepik.

11. Agathis robusta (MOORE) BAILEY, Synops. Queensl. Fl. (1883) 498; WARB. Monsunia 1 (1900) 185; BAKER & SMITH, Pines of Austr. (1910) 376; DALLIMORE & JACKSON, Handb. Conif. (1923) 148; FRANCO, An. Inst. Sup. Agron. 18 (1951) 105, f. 2–10; HYLAND, Brunonia 1 (1978) 105, f. 1; SILBA, Phytologia Mem. 8 (1986) 37. — *Dammara robusta* MOORE *ex* F.v.M. Quart. J. Trans. Pharm. Soc. Vict. 2 (1806) 173. — *Dammara palmerstonii* F.v.M. Vict. Natur. 8 (1891) 45. — *A. palmerstonii* (F.v.M.) BAILEY, Queensl. Dept. Agric. Bot. Bull. 3 (1891) 17; DALLIMORE & JACKSON, Handb. Conif. (1923) 147. — *A. robusta var. robusta* WHITM. Pl. Syst. Evol. 135 (1980) 63. — *A. robusta var. nesophila auct. non* WHITM.: WHITM. *l.c.* f. 6.

Tree to 48 m. *Juvenile leaves* ovate and acuminate, up to 13 by 3.8 cm. *Adult leaves* ovate and acute to rounded at the apex, 5–9.5 cm by 10–26 mm, tapering to a 3–10 mm petiole. *Mature pollen cones* 4–8.5 cm by 7–9 mm, subtended by a 2–9 mm peduncle, apex of microsporophyll sharply angled to form three lateral facies, *c.* 1 mm wide and long, the slightly angled along its margin front (apical) face directed inward to the bases of the next microsporophylls ahead on either side. *Seed cone* oval to elongated, 9–15 by 8–10 cm. *Seed bract* with a thin sharp ridge along the apical margin, rounded at the upper corners, the curving lateral margins with a larger scallop *c.* 10–12 mm above the base on one side and a smaller one 5–8 mm above the base on the other side, 30–45 by 39–46 mm. *Seed c.* 10 by 6 mm with a long acute projection on one upper corner and a long bent wing *c.* 30 by 12 mm at the other.

Distr. In four localized clusters, one in the central part of New Britain, another east of Port Moresby in Papua New Guinea, the largest in the rainforests of northern Queensland, and the last in southern Queensland on Fraser I. and the nearby mainland. Fig. 86.

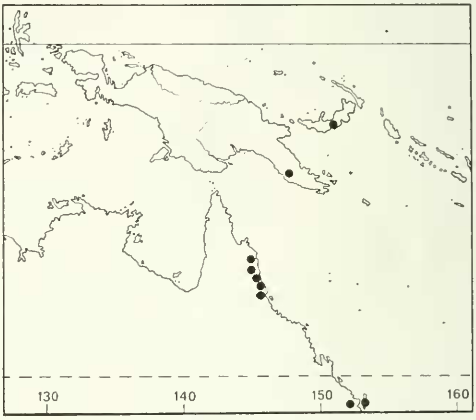

Fig. 86. Range of *Agathis robusta* (MOORE) BAILEY.

Ecol. Locally common on a variety of soils in exposed positions following disturbance from near sea-level in Australia and 400 m further north to 900 m throughout its range.

Vern. *Naveil*, New Britain.

CUPRESSACEAE

Both *Cupressaceae* and the closely related *Taxodiaceae* are important Holarctic families which also have representatives in the southern hemisphere. A few species of both extend into habitats on the margins of the tropics or into tropical highlands. Of 18 genera of *Cupressaceae* only *Libocedrus* reaches into Malesia. Occasional reports of *Callitris* in New Guinea have been based on similar appearing specimens of *Casuarina*.

1. LIBOCEDRUS

ENDL. Syn. Conif. (1847) 42; CARR. Traité Gén. Conif. (1855) 84; MASTERS, J. Linn. Soc. Bot. 30 (1895) 20; WARB. Monsunia 1 (1900) 189; DALLIMORE & JACKSON, Handb. Conif. (1923) 300; LI, J. Arn. Arb. 34 (1953) 17; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 31; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 145; SILBA, Phytologia Mem. 8 (1986) 108. — *Libocedrus subg. Eulibocedrus* PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 389. — *Papuacedrus* LI, J. Arn. Arb. 34 (1953) 25; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 31; BOUTELJE, *l.c.* 198, t. 4, pl. 7 & 8; VAN ROYEN, Alp. Fl. New Guinea 2 (1979) 1. — *Austrocedrus* FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 28. — **Fig. 88, 89.**

Monoecious evergreen trees or shrubs. Bark smooth but fissured, peeling in strips or flakes, fibrous, rich brown but weathering to blackish or gray. *Leaves* in alternating whorls of 3 or 4 soon reduced to opposite decussate, those of the seedling single veined and linear, *c.* 1 cm long, changing abruptly on lateral branches and throughout mature trees to specialized scale forms. *Scale-bearing branches* with small dorsally keeled facial scales alternating decussately with larger marginal leaves that are strongly bilaterally flattened and sometimes extend outward wing-like, the basal margins of each pair meeting between the succeeding facial leaves, the whole branch system further differentiated dorsiventrally with a convex upper surface bearing few or even no stomata and a concave lower surface where the stomata are concentrated, the leaf differentiation diminishing (or more or less disappearing) on older more exposed plants. Foliage buds nothing more than the last pair of developing leaves. *Fertile structures* solitary, terminal, often on short lateral branches. *Pollen cones* cylindric, composed of decussate or more or less crowded scales each with 2–6 inverted pollen sacs. *Seed cones* woody, composed of two oval opposed fertile scales each bearing two erect ovules at their bases and two small triangular lateral sterile scales. The bracts are mostly fused to the outer surface of the scales, the apex of the bract a short to elongated acute spreading projection. *Seed* an elongated cone with two very unequal wings, a narrow wing along one side and an elongated more or less expanded wing at least twice as long as the seed on the other side and extending beyond and more or less outward from the seed apex (micropyle).

Distr. There are 7 *spp.* of Antarctic forests and tropical highlands including New Guinea, New Caledonia, New Zealand, and S. Central Chile with adjacent parts of Argentina. In *Malesia*: 1 *sp.* with 2 varieties endemic to New Guinea and nearby islands. Fig. 87.

Fossils. Foliage shoots and wood from the Eocene of Patagonia and Chile (FLORIN, K. Svenska Vet. Ak. Handl. II, 19, *nr.* 2, 1940, 82).

Ecol. A wide range of forest and rain-forest habitats from lowland tropics to the tropical tree line and throughout the Antarctic forests (in Chile prospering on the dry margins of the forest). Pollination and seed dispersal strictly by wind. Seedlings germinating in abundance in rich humous soils.

Uses. The aromatic wood is similar to that of *Juniperus* in appearance and uses, with light coloured sapwood and reddish brown to purplish heartwood. Where large enough it is much appreciated for construction and furniture while the bark is sometimes used for roofing.

Fig. 87. Range of the genus *Libocedrus* ENDL. with the number of species, all endemic.

Notes. The relationships of *Libocedrus* are emphatically with the Holarctic *Thuja* group of genera (*Tjujoideae*) within *Cupressaceae* making it phytogeographically much like the everywhere associated *Nothofagus* whose relatives are also in the north. Like the other members of *Thujoideae*, the leaves are strongly differentiated into lateral and facial types and even further like many of these genera the branches are also differentiated dorsiventrally (the Holarctic genus *Calocedrus* was for a long time included within *Libocedrus*). Attempts as in LI (1953) to attach *Libocedrus* to southern hemisphere cypresses (*Callitroideae*) by ignoring the highly specialized foliage forms and describing the seed cones as 'valvate' are inadmissible. The so-called valvate appearance is due to the few cone scales, the lowermost scales of any Cupressaceous seed cone being the same so that this appearance occurs wherever the number of scales is reduced, as in *Chamaecyparis nootkatensis*.

The species of New Guinea and of Chile have been placed into separate genera based on slight differences. The upper surface of the leaves of the Chilean species are so constricted that little or no space is left for stomata, making them more or less hypostomatic while other species are clearly amphistomatic but with rather few upper stomata. The New Guinea species was separated on the basis of spirally placed microsporophylls. In fact, simple opposite decussate pollen cones occur alongside crowded cones whose microsporophylls appear to be whorled or perhaps spirally placed. FLORIN & BOUTELJE (1954) carefully examined these cones and found each two decussate pairs of microsporophylls brought to the same level but certainly not spirally placed. On the other hand, they adduced some other minor distinctions for the New Guinea material, in particular that the stomate bands are more or less separated by narrow irregular stomate-free zones, a character not seen elsewhere in the genus. In my opinion these otherwise very similar species should not be separated generically by such unimportant distinctions.

1. Libocedrus papuana F.v.M. Trans. R. Soc. Vict. n.s. 1 (1889) 32; WARB. Monsunia 1 (1900) 189; K.SCH. & LAUT. Fl. Schutzgeb. Südsee (1901) 156; Nachtr. (1905) 51; KOORD. Nova Guinea 8 (1911) 613; LAUT. Bot. Jahrb. 50 (1913) 52, f. 2A–G; LANE-POOLE, For. Res. Terr. Papua New Guinea (1925) 74; SILBA, Phytologia Mem. 8 (1986) 109. — *Thuja papuana* (F.v.M.) Voss, Mitt. Deut. Dendr. Ges. 1907 (1908) 88. — *L. torricellensis* SCHLTR *ex* LAUT. Bot. Jahrb. 50 (1913) 52, f. 2H–N. — *Papuacedrus papuana* (F.v.M.) LI, J. Arn. Arb. (1953) 25; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 32, pl. 2, t. 1–3; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 323; VAN ROYEN, Alp. Fl. New

Fig. 88. View south over the Archbold Expedition camp and Lake Habbema to snow-capped Mt Wilhelmina, from an altitude of 3265 m. Open forest of *Libocedrus papuana* F.v.M. in foreground centre and big, moss-cushioned *Podocarpus compacta*; alt. of Lake Habbema 3225 m, Mt Wilhelmina 4750 m (Photogr. L.J.BRASS, August 1938).

Guinea 2 (1979) 2, f. 33. — *Papuacedrus torricellensis* (SCHLTR) LI, J. Arn. Arb. 34 (1953) 25; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 31, pl. 2, t. 4–6; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 323. — **Fig. 88, 89.**

Trees 2–50 m tall, rarely shrubby, pyramidal or spreading or even slightly pendulous with age. *Leaves* on older and more exposed trees becoming quite small, facial scales rhomboidal, acute, up to half as long as the lateral scales, *c.* 1 mm long, the lateral scales nearly straight, their base between the outermost edges of the next lower facial scales, spreading slightly and then straight or weakly convex, tips extending slightly beyond the outermost edges of the next higher facial scales and either straight or slightly spreading or (when convex) slightly incurved and ± touching the base of the next lateral leaves but below the tips of the next facial leaves, down to *c.* 2 mm long. Branches darker above and often glaucous below. *Pollen cones* 4–25 mm long by 2–3 mm in diameter, the upper part of the microsporophyll roughly triangular, *c.* 1.5 mm long, with 2–4 pollen sacs. *Seed-bearing scale* broadly lanceolate to almost elliptic, at least slightly rounded at the tip, 8–12 mm long and 4–6 mm wide, narrowing at the base and sometimes slightly constricted along the side where touched by the smaller lateral scales which are about half as long and ± lanceolate. *Bracts* broadly fused to the dorsal side of their corresponding scale on its lower half with a short spreading acute to obtuse tip. The woody mature *cone* brown or blackish, often with ridges radiating from the bracts to the margins of the scale. *Seed* 2–3 mm long, the wing twice as long and spreading upward with a bend partway along the outer edge towards the straight inner edge forming an acutish rounded apex.

var. **papuana**

Apex of lateral leaves becoming widely spreading on young plants up to 6 mm from the stem and often

Fig. 89. *Libocedrus papuana* F.v.M. *var. papuana*. A. sterile twig; B. fertile twig; C. pollen cone; D. seed cone; E. scales with pollen sacs (from LAUT. Bot. Jahrb. 50, 1913, 52, f. 2).

falcately bent outwards but the tip always turned upwards, up to 13 mm from base to tip, gradually becoming smaller and less spreading as the tree matures.

Distr. *Malesia*: most of the length of New Guinea along the central range but also on the Huon Peninsula, the Torricelli Mts, and the Cycloop Mts, grading into the other variety towards the western end of New Guinea, particularly at higher elevations. Fig. 90.

Ecol. A tree of mountain rain-forests and especially the mossy forest from 1500 m to the tree line in the central range, sometimes emerging from the alpine scrub to as high as 3800 m, as low as 620 m along the north coast. Above 3300 m a stunted tree less than 10 m tall.

Vern. *Tera*, Garaina; *gamuga, kamgenkuna*, Togoba, Hagen, *ogeleh, oleh*, Chimbu, Masul, *dzagosa, dzasihanini, hanini*, Asaro, Kefamo, *guta, juta*, Mairi, Watabung, *kaibel-kombam, kaipil, ongol*, Wahgi, Minj, *mandilasop, mondalasap, mondolasop, wrenak*, Mendi, *ab, aiap, aip, hap, kap*, Enga, Kepilam, *aioba, hohoba*, Lei area, *bit*, Yogom, *iwunturra*, Manki, *ye-enka*, Nauti, *sukou*, Wapi, Migote.

var. **arfakensis** (GIBBS) DE LAUB., *stat. nov.* — *L. arfakensis* GIBBS, Arfak (1917) 84, f. 6a, b; DALLIMORE & JACKSON, Handb. Conif. (1923) 301; SILBA, Phytologia Mem. 8 (1986) 108. — *Papuacedrus arfakensis* (GIBBS) LI, J. Arn. Arb. 34 (1953) 25; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 32,

Fig. 90. Range of *Libocedrus papuana* F.v.M. *var. papuana* (dots) and *var. arfakensis* (GIBBS) DE LAUB. (triangles).

t. 3; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 322.

Apex of lateral leaves at first spreading but soon constricted to the position on older trees close to the base of the following facial leaves but between their base and tip the lateral leaves expanded outward as much as 3 mm and overall as much as 10 mm long, thus producing a strongly convex shape, gradually becoming smaller until they become indistinguishable from the type variety on older and exposed trees.

Distr. *Malesia*: from the Wissel Lakes through the Vogelkop Peninsula and probably including the material from Batjan and Ternate. Fig. 90.

Ecol. Like the type variety from 1600 to 2500 m, but as low as 840 m along the north coast of the Vogelkop Peninsula.

Vern. *Autibo, dautibo, dautie, matu, matudautie*, Kepauko, *wonga*, Arfak area, *bootsjeka, butsga*, Manikiong, *pomoan*, Manikiong, Hattam, *duwak, nipau, tuwa*, Kebar, *sowa, swa*, Kebar, Andjai, *araum, eis*, Karoon.

Note. Despite the strikingly different juvenile leaves, intermediate specimens exist, especially at higher elevations and it has not been possible to separate specimens taken from older plants.

PINACEAE

The pine family is one of the most characteristic families of the holarctic realm of which family a few genera reach the margins of the tropics in highlands, but only *Pinus* extends into tropical lowlands including Malesia.

1. PINUS

LINN. Gen. Pl. ed. 1 (1737) 731; Sp. Pl. (1753) 1000; LAMBERT, Pinus (1803); PARL. in DC. Prod. 16, 2 (1868) 378; ENGELMANN, Trans. St.Louis Acad. Sc. 4 (1880) 161; MASTERS, J. Linn. Soc. 35 (1904) 560; SHAW, Publ. Arn. Arb. 5 (1914) 24, t. 1–39; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 331, t. 177, 178; GAUSSEN, Gymn. Act. & Foss. fasc. 6 (1960) 11, t. 324–369, pl. 24–29; MIROV, Genus Pinus (1967); SILBA, Phytologia Mem. 8 (1986) 129. — **Fig. 91–93.**

Evergreen monoecious trees or rarely shrubs. Bark smooth or rough, particularly on older trees, peeling in flakes often of very irregular shape. *Leaves* linear or lanceolate, often with minute serrations, spirally placed, soon replaced by scales in the axils of which appear reduced shoots in the form of bundles enclosed around their base by a sheath of scale leaves, adult leaves in the bundles linear, pungent, needle-like, the cross section of each leaf forming a sector of the circle formed by the entire bundle. *Pollen cones* numerous, axillary, cylindrical, subtended by a cluster of overlapping scales similar to the foliage bud, microsporophylls scale-like with two inverted pollen sacs. *Seed cones* terminal

Fig. 91. *Pinus merkusii* JUNGH. & DE VRIESE in primary forest habitat on slope of Mt Bandahara, Leuser Nature Park, Sumatra, 2000 m alt. (Photogr. W.J.J.O. DE WILDE, 1972).

on short scaly shoots, more or less cylindrical, consisting of numerous fertile scales which become woody, ripening in the second or third year, the apiculate bract fused with the scale, two inverted ovules on each scale. *Seed* egg-shaped, with a firm outer shell, usually with an expanded wing which is attached to the broad base of the seed.

Distr. Over one hundred species across the middle and higher latitudes of the northern hemisphere and southward into Central America, Cuba, and Hispaniola as well as into *Malesia*, where two important pines of southeastern Asia (belonging to *subg. Diploxylon*) extend their range. Absent from the Indian subcontinent, but occurring throughout the Himalayan range.

Fig. 92. *Pinus merkusii* JUNGH. & DE VRIESE in fire-prone grassland, blang area along the Gajo-road, Sumatra (Photogr. J.C. VAN DER MEER MOHR, 1925).

Ecol. A wide range of forest and savanna habitats most characteristically following disturbance and thus even as large trees surrounded by rain-forest in some cases. Frequently occurring as a fire climax woodland or scattered in fire-prone grasslands. Pollination and seed dispersal by wind or in many cases the seed are gathered by birds or rodents or even collected for human food.

Note. Pines are leading sources of lumber and pulpwood and some species such as the two described here yield large amounts of pitch and are tapped to make turpentine. Use as ornamentals is widespread and pines are favourite subjects of afforestation. The widespread use of pines in tropical tree plantations derives from the detailed information available for their silviculture and not because they are of particularly good quality wood. The fact is that much tropical pine wood production is of very poor quality and it is to be hoped that knowledge of the production of better quality woods will increase in the future.

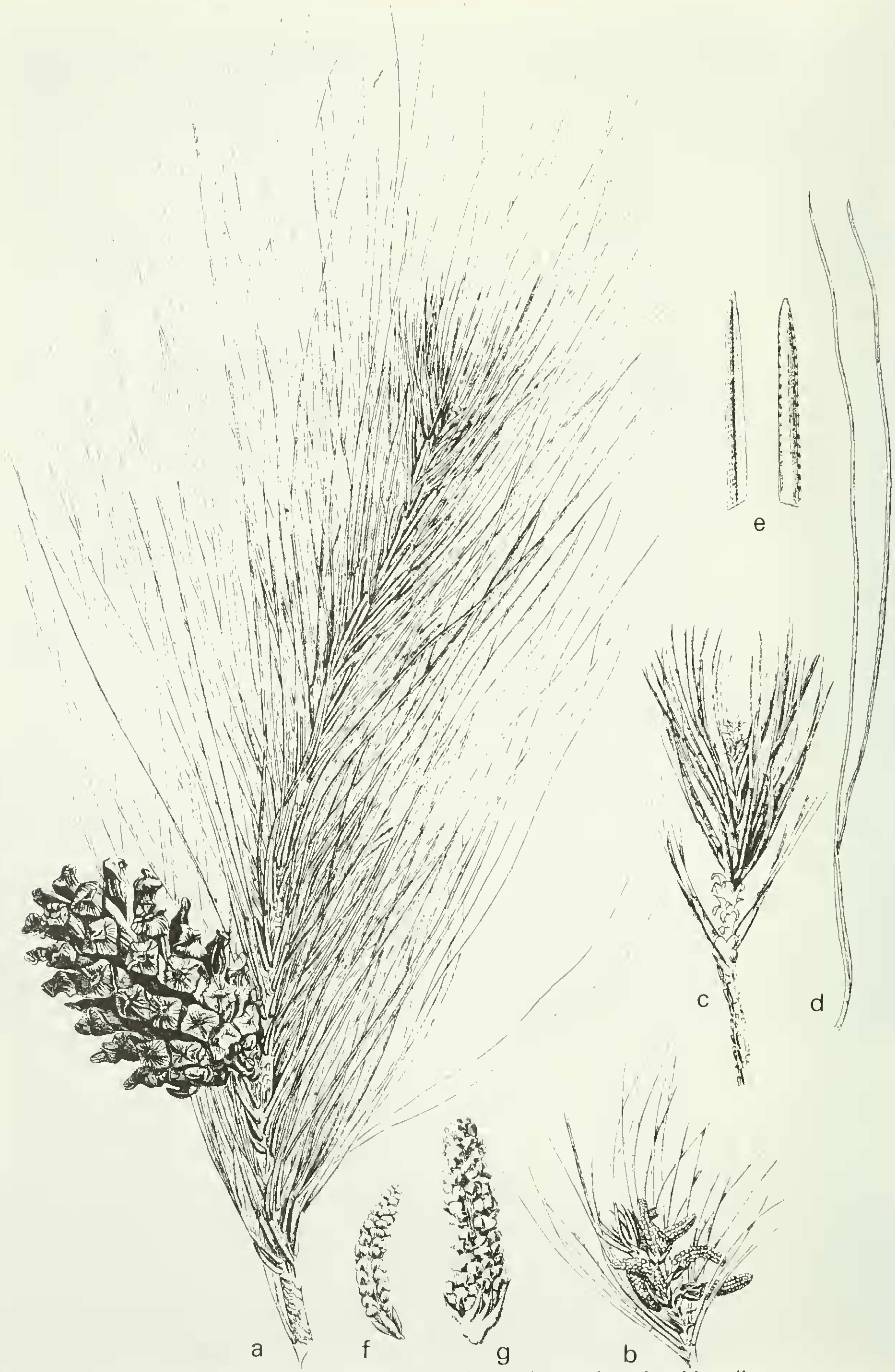

Fig. 93. *Pinus merkusii* JUNGH. & DE VRIESE. a. Twig with seed cone; b. twig with pollen cones; c. growing shoot; d. pair of needles; e. tips of needles, enlarged; f, g. pollen cones (from DE VRIESE, Pl. Nov. Ind. Bat. Or., 1845, 5, t. 2).

KEY TO THE SPECIES

1. Leaves two per bundle. Mature seed cone ovate .... 1. P. merkusii
1. Leaves three per bundle. Mature seed cone globular .... 2. P. kesiya

1. Pinus merkusii JUNGH. & DE VRIESE in De Vriese, Pl. Nov. Ind. Bat. Or. (1845) 5, t. 2; Bot. Zeit. 4 (1846) 13; ENDL. Syn. Conif. (1847) 176; CARR. Traité Gén. Conif. (1855) 380; GORDON, Pinetum ed. 1 (1858) 169; MIQ. Fl. Ind. Bat. 2 (1859) 1069; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 43; DE BOER, Conif. Archip. Ind. (1866) 5; PARL. in DC. Prod. 16, 2 (1868) 389; VIDAL, Sin. Atlas (1883) 43, t. 98, f. B; Rev. Pl. Vasc. Filip. (1886) 296; MERR. For. Bur. Bull. Philip. 1 (1903) 15; FOXW. Philip. J. Sc. 6 (1911) Bot. 169; SHAW, Publ. Arn. Arb. 5 (1914) 23, t. 198–200; DALLIMORE & JACKSON, Handb. Conif. (1923) 415; GAUSSEN, Gymn. Act. & Foss. fasc. 6 (1960) 146, t. 344, 2 & 3; CRITCHF. & LITTLE, U.S. Dept. Ag. Misc. Publ. 991 (1966) 15, map 39; MIROV, Genus Pinus (1967) 284, f. 3-51-52, t. 3-68-69, 553; COOLING, Fast Growing Timber Trees Low. Tropics 4 (1968) 126; STEEN. Fl. Males. Bull. *n.* 25 (1971) 1948; PHENGKLAI, Thai For. Bull. 7 (1973) 1, f. 1; SILBA, Phytologia Mem. 8 (1986) 149. — *P. sylvestris auct. non* L.: LOUR. Fl. Coch. 2 (1790) 579. — *P. sumatrana* JUNGH. Bot. Zeit. 4 (1846) 698. — *P. finlaysoniana* BLUME, Rumphia 3 (1849) 210. — *P. latteri* MASON, J. Asiat. Soc. 1 (1849) 74. — *P. merkusii var. tonkinensis* CHEV. Rev. Bot. Appl. Ag. Trop. 24 (1944) 7. — *P. merkusiana* COOLING & GAUSSEN, Trav. Lab. For. Toulouse (1970) 1. — **Fig. 91–93.**

Fig. 94. Range of *Pinus merkusii* JUNGH. & DE VRIESE.

Large tree 40–50 m tall, occasionally to 70 m. Pyramidal with heavy horizontal branches and thick fissured bark in most areas but in some regions trees have more slender, somewhat ascending branches and much thinner, smoothish bark resembling that in the upper crown of thick-barked populations. These two types hold true in artificial plantings. The reddish bark of young trees changes to dark brown weathering to gray on older trees. *Foliage buds* long and narrow with awl-shaped scales. *Needles* in pairs, 16–19 cm by 1 mm, abruptly pointed, stomata on all faces, falling in the second year. Basal sheath 12–18 mm long, reddish. *Pollen cones* 18–25 by 5 mm. *Seed cone* cylindrical before opening, 5–11 by 3 cm and twice as thick after opening, generally falling soon after shedding seeds. *Apophysis* broadly tetragonal in shape with a smooth, almost depressed umbo. *Seed* 7.5 by 4.5 mm, with a deciduous wing 25 by 8 mm.

Distr. In *Malesia* common throughout the mountains of Atjeh in Sumatra and scattered further south in Tapanuli with an isolated outlier near Mt Kerintji at *c.* 2° south of the equator and the only natural occurrence of pine south of the equator. The same or a closely related pine is scattered throughout SE. Asia from E. Burma to the South China Sea and two small areas in the Philippines, one on Mindoro and the other near the west coast of Luzon in Zambales Prov. Fig. 94.

Ecol. From low elevations to 2000 m, generally on poor quality acid podzolic soils over sandstone or fresh volcanic ash, sometimes on deeply leached acid basalt, rarely successfully competing on richer forest soils. Most stands show a clear relationship to fire or other disturbance and the pine can be seen to be expanding in recently disturbed areas. In Sumatra the habitat experiences heavy year-round precipitation, but the pine areas themselves definitely favour the drier sites. The Tapanuli populations, which have thin bark, are more sensitive to fire and do not descend below 1000 m. Elsewhere, including the Philippine islands, this pine grows in strongly seasonal environments.

Vern. Sumatra: *dammar batu, dammar bunga, hejam, hujam, ujam, ujem*, Atjeh, *higi*, Kerintji, *kaju tussam, tussam*, Battok, Tapanuli; Philippines: *tapulao*, Sambal, Luzon, *agoo, aguu, salit*, Philip. islands.

Note. The similar pines of the southeastern Asian mainland and the Philippines differ in certain ways from those of Sumatra. The mainland pines, which grow in areas with a distinct dry season much stronger than any seasonality in Sumatra, have a distinct grass stage for the seedling, a character not seen at all in Sumatra. The needles are 19–24(–27) cm long, the seed cones have a more typical taper of most pines, not the unusual cylindrical Sumatran shape, and their umbos tend to be distinctly raised on an apophysis distinctly wider than high. Seeds are nearly twice as heavy. Sumatran pines have a multinodal leader (several nodes in each year's growth) while the mainland form is uninodal. The new species, *P. merkusiana*, proposed for the mainland population, was described without a type specimen, but the earlier name, *P. latteri*, is already available. The varietal name *tonkinensis* is also available. Like Sumatra, mainland areas have an 'upland' thin-barked form to which the varietal name applies should further nomenclatural divisions be needed.

2. Pinus kesiya ROYLE *ex* GORDON in Loudon, Gard. Mag. 16 (1840) 8; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 436; STYLES & BURLEY, Comm. For. Rev. 51 (1972) 241; BURLEY, Proc. IUFRO Breeding Symp. Gainesville (1972) 38; PHENGKLAI, Thai For. Bull. 7 (1973) 3; QUIMBO, Canopy 4 (9) (1978) 9, 14; PADOLINA, Canopy 4 (10) (1978) 5; STYLES, Canopy (Aug. 1979) 5; in Armitage & Burley, Trop. For. Pap. 9 (1980) 199. — *P. taeda auct. non* L.: BLANCO, Fl. Filip. (1837) 767; MERR. Bur. Govt. Lab. Publ. Philip. 27 (1905) 82. — *P. insularis* ENDL. Syn. Conif. (1847) 157; PRESL, Epim. Bot. (1851) 37; PARL. in DC. Prod. 16, 2 (1868) 390; VIDAL, Sin. Atlas (1883) 43, t. 98, f. C; Rev. Pl. Vasc. Filip. 1 (1903) 15; Philip. J. Sc. 5 (1910) Bot. 325; WHITF. For. Bur. Bull. 10 (2) (1911) 26, t. 2, 3; FOXW. Philip. J. Sc. 6 (1911) Bot. 170; SHAW, Genus Pinus (1914) 60, t. 23, f. 208–210; WU, Acta Phytotax. Sinica 5 (1956) 145; RAIZADA & SAHNI, Ind. For. Rec. 5 (1960) 114, t. 5, f. 3; BACK. & BAKH. *f.* Fl. Java 1 (1963) 91; CRITCHF. & LITTLE, U.S. Dept. Ag. Misc. Publ. 991 (1966) 14, map 38; MIROV, Genus Pinus (1967) 297; ROJO, Sylvatrop 3 (1978) 31; DE LAUB. Kalikasan 7 (1978) 148; ROJO, Canopy (March 1979) 10; SILBA, Phytologia Mem. 8 (1986) 145. — *P. khasyana* GRIFF. Notul. Pl. Asiat. 4 (1854) 18, t. 367, 368, with ref. to descr.: 2 (1848) 58. — *P. kasya* PARL. in DC. Prod. 16, 2 (1868) 390; BRANDIS, For. Fl. NW & Central India (1874) 508; KURZ, Fl. Burma 2 (1877) 499; GAMBLE, Man. Ind. Timber (1881) 397. — *P. khasia* ENGELMANN, Trans. St. Louis Acad. Sc. 4 (1880) 179. — *P. khasya* HOOK. *f.* Fl. Br. India 5 (1888) 652; GAMBLE, Man. Ind. Timber 2 (1902) 708; MERR. For. Bur. Philip. 1 (1903) 15; BRANDIS, Indian Trees (1906) 690; DALLIMORE & JACKSON, Handb. Conif. (1923) 400; BUIC NGOC-SANH, Adansonia 2 (1962) 337; GAUSSEN, Gymn. Act. & Foss. fasc. 6 (1960) 154, f. 345, 5, 7, *incl. var. insularis* (ENDL.) GAUSSEN, *l.c.* f. 345, 6; NGUYEN KHA, Ann. Sci. For. 23 (1966) 261; MIROV, Genus Pinus (1967) 295.

Tree to 35–45 m, the crown expanding on older trees. Bark reddish brown, thick and deeply reticulately fissured, breaking off in small thick irregular plates and thus sometimes becoming smoother and plate-like. Branchlets smooth, bright brown. Buds oblong cylindric and non-resinous with brown lanceolate scales free at the tips. *Needles* in threes, rarely pairs, 12–24 cm by 0.5 mm, acuminate, stomata on most surfaces, falling after two years. Basal sheath 5–18 mm long, greyish brown. *Pollen cones* 18–30 by 5 mm. *Seed cone* ovoid to conical before opening, 4.5–10 by 3–5 cm, very persistent. *Apophysis* wider than long, pyramidal, the umbo with a small expanded and usually deciduous mucro. *Seed* 5–8 by 3 mm with a deciduous wing 20 by 8 mm.

Distr. Across SE. Asia to E. India (Khasia) and a short way into China; in *Malesia*: Philippines (common in the northern part of Luzon). Fig. 95.

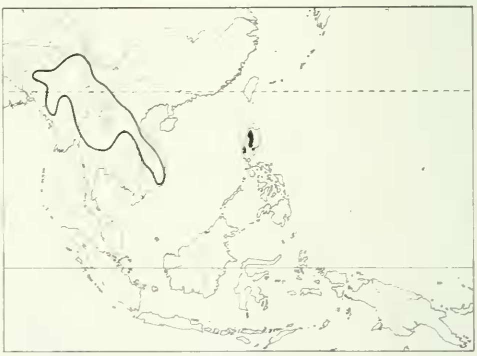

Fig. 95. Range of *Pinus kesiya* ROYLE *ex* GORDON.

Ecol. Most often in open pure stands following fire, but also mixed with oaks and Ericaceous species at intermediate elevations from 300 to 2700 m, often on steep slopes. Generally in the same area as *P. merkusii*, but usually at higher elevations. A few specimens in the Philippines have been considered hybrids between these two species, but actual hybridization has not been verified.

Vern. *Al-al, parua, saleng*; *boo boo, bot bol, bulbul*, If., *tapulao*, Zambales.

Note. *Pinus timorensis* (an earlier name) was thought by some to be equal to *P. kesiya* (*P. insularis*) although the description is inadequate to confirm this. There are no native pines in Timor; perhaps this was a cultivated tree.

Doubtful or Excluded

Callitris sp. mentioned from New Guinea by H.J.LAM, Nat. Tijd. Ned. Ind. 89 (1929) 304, 354; Sargentia 5 (1945) 143, 168, is according to VAN STEENIS, Acta Bot. Neerl. 2 (1953) 299 = *Gymnostoma sp.* (*Casuarinaceae*).

Podocarpus elata R.BR. — ENGLER, Bot. Jahrb. 7 (1886) 445, mentioned a specimen from Timor (Kupang Bay) to belong to this Australian species. PILGER did not mention this specimen in his monograph and WASSCHER did not see it either (*cf.* Blumea 4, 1941, 471).

Podocarpus palembanica MIQ. Fl. Ind. Bat. Suppl. (1860) 252, 289. According to DE BOER (Conif. Arch. Ind., 1866, 4) it is not a conifer because of its non-coniferous wood. KOSTERMANS (Reinwardtia 2, 1953, 362) observed its stipules and nerves and identified it as a juvenile specimen of *Ganua sp.*, later referred tentatively to a distinct species by VAN DEN ASSEM (Blumea 7, 1954, 482): *Ganua palembanica* (MIQ.) VAN DEN ASSEM & KOSTERM. (*Sapotaceae*).

Thuja javanica BURM. *f.* Fl. Ind. (1768) 202, t. 64, f. 3. — *Podocarpus javanicus* (BURM. *f.*) MERR. Philip. J. Sc. 19 (1921) 338, *pro nomen*. BURMAN's description and figure are based on a specimen of Java. In L there is a specimen in herb. VAN ROYEN, with a label *'Thuya javanica è Java. Monoic.'* which seems to be in BURMAN's handwriting and which can provisionally be accepted as the type specimen. According to HALLIER *f.* (Meded. Rijksherb. *n.* 37, 1918, 92) it belongs to *Juniperus chinensis*, a conifer already cultivated in Java in early days.